PHYLOGENETIC ANALYSIS OF CIMICOMORPHAN FAMILY RELATIONSHIPS (HETEROPTERA)

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Abstract.—A cladistic analysis of the Cimicomorpha is conducted, including 19 family-level terminal taxa and 51 characters with 127 states. The literature is reviewed and found to contain much relevant character information on gross morphology and attributes of reproduction. Previous classificatory efforts, individual characters, and new morphological information are discussed. The following sequenced classification is proposed: CIMICOMORPHA—Reduvioidea (Pachynomidae, Reduviidae); Velocipedoidea (Velocipedidae); Miriformes (Microphysoidea: Microphysidae; Joppeicoidea: Joppeicidae; Miroidea: Thaumastocoridae, Miridae, Tingidae); Cimiciformes (Naboidea: Medocostidae, Nabidae; Cimicoidea: Lasiochilidae, Plokiophilidae, Lyctocoridae, Anthocoridae, Cimicidae, Polyctenidae).

The advent of cladistics has had a profound impact on the classification of many groups, including the Heteroptera. However, many taxa have never been the subject of a detailed cladistic analysis. Schuh (1986) in a review of the subject, placed about half of the families of Cimicomorpha as *incertae sedis* because there was only one detailed analysis of all families (Kerzhner, 1981), and several of the included groups were obviously paraphyletic. Our interest in developing a comprehensive classification of the Heteroptera based on the recognition of monophyletic groups, and the opportunity to work collaboratively at the same institution, led us to this attempt at a phylogenetic classification of the Cimicomorpha.

The present paper is organized as follows: history of classification of the Cimicomorpha; brief characterization of terminal taxa used in our analysis and arguments for their monophyly; sources of character information; discussion of phylogenetic methods and results with character descriptions and a character matrix; comparison of previous and current results; classification of the Cimicomorpha; and an appendix explaining individual characters and discussion of their interpretation. Also included are figures of the labium and mesothoracic wings, cladograms of previous and current phylogenetic schemes, and character states trees for multistate characters.

The extensive work of Jacques Carayon on the morphology, anatomy, and reproduction in nearly all families of Cimicomorpha forms the foundation for much of our analysis. Without his work only a relatively superficial listing of characters would be possible. It is clear that our attempts at synthesis differ greatly from those of Carayon. This appears to result from our efforts to view characters in a transformational framework. Such an approach allows character information to be construed hierarchically, and more effectively portrayed in a phylogenetic context. Furthermore,

in our attempts to produce a phylogenetic classification, we have rejected paraphyletic groups and attempted to form all groupings on the basis of synapomorphy.

DEDICATION

This paper is written in honor of our longtime friend and colleague James A. Slater. Such recognition seems fitting, because in addition to his voluminous and seminal contributions on the Lygaeidae, his first major work on the Heteroptera concerned the Cimicomorpha, more particularly the significance of the female genitalia in the classification of the Miridae. Of still greater importance for understanding broad-scale relationships within the Cimicomorpha are his contributions on the Thaumastocoridae. On a more personal level we have always benefited from his interest in our own work, in the form of straightforward encouragement, exchange of ideas, and critical commentary. His distinguished and productive career has long served as an example, and we wish him many more productive years of enjoying his interest in the Heteroptera.

HISTORY OF CLASSIFICATION OF THE CIMICOMORPHA

The traditional classification of Dufour (1833) divided the Heteroptera into the Geocorisae, Hydrocorisae (now Nepomorpha), and Amphibicorisae (now Gerromorpha); recently it has become clear that only the last two groups are monophyletic (Rieger, 1976, and Andersen, 1982, respectively). Identification of monophyletic subgroups within the Geocorisae has been a gradual process, the major breakthroughs coming with the recognition of the Trichophora by Tullgren (1918) and later the recognition of the Pentatomomorpha (Aradidae + Trichophora) and the Cimicomorpha by Leston, Pendergrast and Southwood (1954) (for a review and presently accepted classification see Štys and Kerzhner [1975], Schuh [1986], and Insects of Australia [1991]). The Cimicomorpha as conceived by Leston, Pendergrast and Southwood (1954) is very similar to that used in this paper, except that they did not mention in which higher group the Thaumastocoridae were to be placed. The Thaumastocoridae were unequivocally associated with the Cimicomorpha by Drake and Slater (1957). The Vianaidinae (Kormilev, 1955b) were included in the Cimicomorpha, and more particularly in the Tingidae, by Drake and Davis (1960), and the Medocostidae were described and added to the group by Štys (1967a).

Some modern authors have conceived the Cimicomorpha in the same sense as Leston, Pendergrast and Southwood (1954), e.g., Miyamoto (1961), Popov (1971), Štys and Kerzhner (1975), Schuh (1979), and Kerzhner (1981), whereas other authors treated the group in a much broader sense, e.g., China and Miller (1959: fig. 1) who included the Dipsocoromorpha and Enicocephalomorpha, Wagner (1961) who included the Dipsocoromorpha, Stichel (1955) who included the Dipsocoromorpha and Leptopodomorpha, and Scudder (1959) who included the Dipsocoromorpha, Gerromorpha, Nepomorpha, and Leptopodomorpha. On the other hand, Cobben (1968, 1978) believed the Reduviidae and Thaumastocoridae must be placed outside the Cimicomorpha, and they (as well as the Pachynomidae) have been consistently omitted by Carayon (1977a, b, 1984) and Péricart (1983). Our arguments for accepting

the Cimicomorpha in the sense of Leston, Pendergrast and Southwood (but also including Thaumastocoridae) are presented below.

Although a number of family trees and narrative arguments concerning relationships within the Cimicomorpha have appeared in the literature over the decades, only two authors have published phylogenetic arguments. Schuh (1979), using data from Cobben (1978), considered the relationships of the Reduviidae, Pachynomidae, and remaining families, and Kerzhner (1981) treated all families currently placed in the Cimicomorpha. Ford (ms) analyzed data published by Carayon for the cimicoid families, and her cladogram and supporting character information were published in Schuh (1986).

TERMINAL TAXA AND ARGUMENTS
FOR THEIR MONOPHYLY

In the following paragraphs we discuss the selection of outgroups used in our cladistic analysis and document the monophyly of the Cimicomorpha and terminal taxa. Examples of characters unique to each terminal taxon are provided, as well as a brief modern history of the classification of the various groups. Characters listed are usually autapomorphies and are not included in our phylogenetic analysis. Additional autapomorphies are listed in the caption to Figure 1.

Outgroups. We have used the Leptopodomorpha and a hypothetical cimicomorphan ancestor as outgroups in our analysis. Characters for the hypothetical ancestor are those found in the ground plan (see also discussion under Phylogenetic Methods). When variation for a given character occurred in the outgroup, we generally coded for the character as it occurs in the presumed ground plan for the Heteroptera. We use the term *ground plan* to mean the character set of the most recent common ancestor of a group. For example, the prepedicellite (character 6) according to Zrzavý (1991) is present in the Saldoidea and absent in the Leptopodoidea. Its absence appears to be part of the heteropteran ground plan (Zrzavý, 1991) and we have therefore coded it in this manner for the Leptopodomorpha.

Schuh (1979) regarded the Pentatomomorpha as the sister group of the Cimicomorpha. We coded a hypothetical pentatomomorphan ancestor in the matrix, but found that it was always treated as part of the Cimicomorpha, rather than an ancestor. This appears to result from the fact that not enough information is contained in our character matrix to correctly relate outgroup taxa such as the Pentatomomorpha, which share many attributes in common with phytophagous Cimicomorpha. Furthermore, there is insufficient information available in the literature to confidently determine the ground plan condition in the Pentatomomorpha for many of the characters used in our study. The question of infraordinal relationships is beyond the scope of this paper, so we have retained the outgroups specified above, because as documented below there is ample evidence showing the Cimicomorpha as monophyletic and no evidence suggesting that one of its subgroups is more closely related to the Pentatomomorpha than to the remaining Cimicomorpha. In the long run, only a study at the infraordinal level will determine whether we have rooted the cladogram correctly or not.

Cimicomorpha. A revised diagnosis of this group indicates that its members possess the following synapomorphies:

1) The ectodermal median spermatheca is nonfunctional as a sperm storage organ

and is either vestigial, modified into a vermiform gland, or entirely absent. Concomitantly, the methods of insemination and sperm storage are diverse and unique among the Heteroptera, sperm often being stored in organs evolved *de novo*. Absence of the spermatheca or its nonfunctionality as a sperm storage organ is shared only with some clearly unrelated members of the Enicocephalomorpha, Dipsocoromorpha, and a few Pentatomomorpha, viz., Aneurinae (Aradidae) (Carayon, 1954, 1955), Idiostolidae (Scudder, 1962; Schaefer, 1966), and some Oxycareninae (Lygaeidae) (Carayon, 1964). We know of no evidence suggesting that a non-functional spermatheca is part of the ground plan of any one of these higher groups. For interpretation of the modified spermatheca see discussion under character support below and of character 43 in the Appendix.

2) Eggs with micropyles which are distinct from aeropyles ("pseudomicropyles") and both arranged in a ring outside the operculum. (For the condition in other groups, see Cobben, 1968.) However, the operculum is absent in the Plokiophilidae, the micropyles are situated on the operculum of some Bryocorinae (Miridae), and are missing in several families (all cimicoid families, Pachynomidae, and Nabinae: Arachnocorini), and the Thaumastocoridae are in many respects aberrant (Southwood, 1956; Cobben, 1968).

Current knowledge of phylogenetic relationships and character distributions within the Cimicomorpha makes the status of other characters considered as synapomorphic by Leston, Pendergrast and Southwood (1954) and Sweet (ms) equivocal. Among these are: characters of the endosoma and basal apparatus of the phallus, course of the radius and media in the hind wing, common presence of the costal fracture, vesicular nature of the accessory salivary glands, common insertion of eggs into plant tissue, and egg rupture by pressure of serosa or embryonic cuticulum combined with the absence of an egg burster. Some of these characters are shared with other higher taxa, part of them being possible characters of the heteropteran ground plan. A few other potential synapomorphies for the Cimicomorpha are discussed below in connection with the results of our phylogenetic analysis.

Reduviidae. This very large world-wide group of predatory bugs has been divided into about 30 subfamilies, but following studies by Davis (1957, 1961, 1966, 1969; and others), the number has been reduced to 23 subfamilies and 33 tribes recognized by Putchkov and Putchkov (1985) and Putchkov (1987) or 25 subfamilies recognized by Maldonado (1990). The Reduviidae has been conceived as a unit by many authors, with the sometime exclusion of the Elasmodeminae and Phymatinae (Wygodzinsky 1944; China and Miller, 1959; Madonado, 1990) as separate families. Arguments for inclusion of the Elasmodeminae within the Reduviidae were made convincingly by Davis (1957) and for the Phymatinae by Carayon, Usinger and Wygodzinsky (1958), the latter argument accepted by Davis (1961), but apparently rejected by Kormilev and Froeschner (1989). Should these two subfamilies be regarded as distinct families, then at least the Holoptilinae, which also belong to the phymatine-elasmodemine clade (Carayon et al., 1958), would also have to be elevated to family rank in order to maintain a monophyletic Reduviidae. Such a splitting might also affect the rank of some other reduviid taxa, because according to Davis (1961) the Phimophorinae, Mendanocorinae, and Centrocneminae also belong to the "phymatine complex." The Emesinae have often been treated as a distinct family, but no modern specialist has done so (see e.g., Wygodzinsky, 1966). Characters distinctive

to the Reduviidae (including Elasmodeminae, Emesinae, and Phymatinae) are: prosternal stridulatory sulcus, distinctive fore and hind wing venation (Davis, 1961), consistent lack of a costal fracture, and presence of paired tubular pseudospermathecae serving the function of the spermatheca (Carayon, 1954) which is transformed into a vermiform gland. Many members of this morphologically diverse group have lost or dramatically modified certain ground plan characters, e.g., the labium is secondarily elongate and flexible in the hematophagous Triatominae and the prosternal stridulatory sulcus has been lost in some genera (Miller, 1956b).

Pachynomidae. Recognized as a family by most modern authors (e.g., Carayon and Villiers, 1968), the Pachynomidae according to Davis (1966) might even be considered as a subfamily of the Reduviidae. They were originally described in the Nabidae by Stål (1873), transferred to the Reduviidae by Carayon (1950a), and elevated to family rank by Carayon (1954). The group is pantropical with four described genera, placed in two subfamilies by Carayon and Villiers (1968): Pachynominae (*Camarochilus* Harris, 1930; *Pachynomus* Klug, 1830; and *Punctius* Stål, 1873) and Aphelonotinae (*Aphelonotus* Uhler, 1894). Its members are distinguished by their possession of trichobothria on either side of the ventral abdominal midline. In addition to a small and relatively inconspicuous prepedicellite, they have 5-segmented antennae, owing to fragmentation of the pedicel into 2 segments (as in the Pentatomoidea) combined with the occurrence of an intersegmental intrapedicelloid between the segments, which is unique among the Heteroptera (Zrzavý, 1991); the single antennal trichobothrium occurs on the distal subdivision of the pedicel (see also discussion under Prostemmatinae and character 6 in the appendix). The general facies and structure of the forewing are extremely diverse; for example, the costal fracture may be present or absent and the membrane venation may resemble that of the Nabidae or Reduviidae. The life habits are virtually unknown, and this appears (in addition to the Medocostidae) to be the only group of cimicomorphans for which larvae have never been collected.

Velocipedidae. Because of their possession of a peculiar combination of characters the members of this group have been placed in various higher groups of different ranks over time. The only genus, *Scotomedes* Stål 1873 (=*Velocipeda* Bergroth, 1891, *Godefridus* Distant, 1904), with a subgenus *Bloeteomedes* van Doesburg, 1970, was originally placed in the Nabidae (Stål, 1873), by some authors in the Saldidae (Bergroth, 1891), and later treated as a distinct family (Velocipedidae) of doubtful affinities. More recently the group has been treated as a subfamily of the Nabidae by Blöte (1945), Carayon (1970) and Kerzhner (1971, 1981). The few known species are distributed from mainland southeast Asia to New Guinea. The most obvious features unique to the group are the greatly expanded explanate exocorium in the forewing, the extremely elongate third and strikingly abbreviated fourth labial segments (also known in some Lasiochilidae), a very long costal fracture, and the presence of 3 basal, short, closed cells on the membrane with many simple veins emanating from them (Kerzhner, 1981).

Microphysidae. This group of tiny bugs is known from the Palearctic, eastern North America, and Mexico; through the courtesy of D. Jacobs (University of Pretoria) we examined several undescribed species from South Africa (Jacobs and Štys, in prep.), extending the known range into the Southern Hemisphere. At present 5 genera are recognized (*Ciorulla* Péricart, 1974, *Loricula* Curtis, 1833 [=*Microphysa* Westwood,

1834], and *Myrmedobia* Baerensprung, 1857, from the Eastern Hemisphere; and *Chinaola* Blatchley, 1928, and *Mallochiola* Bergroth, 1925, from the Western Hemisphere; see also discussion under Plokiophilidae). Family placement of the Western Hemisphere genera was a matter of dispute following their discovery because there was no general agreement on group-defining characters for many higher taxa of Cimicomorpha. The group is distinguished by: the type of alary sexual dimorphism found in the Old World species, unique venation of the forewing membrane with a single heavily sclerotized cell with a stub distilaterally, and the distal sector of R + M in the hind wing branching into a fork (shared with Nabinae only) (Davis, 1961). Also, the combination of small symmetrical parameres and a long (mirid- or anthocoridlike) costal fracture is diagnostic, although not synapomorphic for the group. Because of the minuteness and rarity of many taxa, details of morphology in the group are still in need of study.

Joppeicidae. This monotypic family contains only *Joppeicus paradoxus* Puton, 1881, a species originally placed in the Aradidae and later transferred to the Lygaeidae by Bergroth (1898), and finally incorporated in the Cimicomorpha by Leston, Pendergrast and Southwood (1954). The group is restricted to northeast Africa and the easternmost Mediterranean (Štys, 1971). Distinctive features include a pronotum with a median longitudinal carina, unique venation of the forewing membrane (Fig. 6F), simplified phallus in the form of an inverted J, and the plesiomorphic (?) presence of a well developed larval scent gland between abdominal terga 6 and 7. The major work on the morphology of the group is that of Davis and Usinger (1970). Carayon (1962a) suggested that insemination takes place in the vitellarium, as in the Cimicoidea (excluding Lasiochilidae), however, Davis and Usinger (1970) documented that it actually takes place in the distal part of the lateral oviducts and the ovariole pedicels.

Thaumastocorinae and Xylastodorinae. (Thaumastocoridae). We recognize the two subfamilies of the family Thaumastocoridae for purposes of this phylogenetic analysis, because although they appear to form a monophyletic group, they differ greatly in certain structures. The family includes the South Indian and Australian Thaumastocorinae (=Thaumastotheriinae) with 4 genera (*Baclozygum* Bergroth, 1909, *Onymocoris* Drake and Slater, 1957, *Thaumastocoris* Kirkaldy, 1908, and *Wechina* Drake and Slater, 1957), and the Neotropical Xylastodorinae (=Discocorinae) with 2 genera (*Discocoris* Kormilev, 1955a and *Xylastodoris* Barber, 1920). The two subgroups possess in common the often greatly expanded mandibular plates, the unique type of asymmetrical male genitalia, and the absence of external genitalia in the female. The Thaumastocorinae possess a structure we refer to as the *tibial appendix,* located distally on the foretibia, but they lack pulvilli. The Xylastodorinae are unique among the Cimicomorpha for the large pentatomomorphan-like pulvilli arising from near the base of the claws but lack the tibial appendix found in the Thaumastocorinae.

The morphology and history of classification of the family is covered by Drake and Slater (1957). Kirkaldy described Thaumastocorinae as a subfamily of Lygaeidae, and Reuter (1912) elevated it to the status of family. Barber (1920) and Kormilev (1955a) described Xylastodorinae and Discocorinae respectively; these Neotropical subfamilies were synonymized by Drake and Slater (1957). Viana and Carpintero (1981) elevated the Xylastodorinae to family status, an idea rejected by Slater and Brailovsky (1983); we agree with the latter authors. Recently Slater and Brailovsky

(1983) and Slater and Schuh (1990) have used the name Xylastodoridinae rather than Xylastodorinae; we have retained the original spelling, in spite of the fact that it might be etymologically incorrect.

Miridae. The Miridae is treated here as including the Isometopinae, following Carayon (1958) and many other subsequent authors. The Isometopinae share all of the ground plan characters of the Miridae except the plesiomorphic presence of ocelli. The family is of world-wide distribution, with 7 to 9 subfamilies and at least 30 tribes (e.g., Carvalho, 1952; Schuh, 1976); with no fewer than 10,000 described species, this is by far the largest family in the Heteroptera. Distinctive for the group are the male genitalia, always having the parameres unequally developed, the left being prominent over the right with very few exceptions, unique membrane venation with 2 cells (more rarely 1), and the several trichobothria on the meso- and meta-femora. Also, the subdivided trochanters appear to be unique. Unlike most families of Heteroptera (except many dipsocoromorphans), the pretarsus shows substantial morphological variation in the Miridae (e.g., Schuh, 1976).

Vianaidinae. Owing to its distinct general facies and unique characters, this group was treated as a family by Kormilev (1955b) at the time of its original description, and later by Scudder (1959), Carayon (1962b), Štys and Kerzhner (1975), and Kerzhner (1981). We have followed Drake and Davis (1960) and Drake and Ruhoff (1965) who treated the group as a subfamily of the Tingidae. The Vianaidinae is a small Neotropical subterranean group containing 2 described genera, viz., *Thaumamannia* Drake and Davis, 1960 and *Anommatocoris* China, 1945 (=*Vianaida* Kormilev, 1955b) (originally placed in the Lygaeidae, Oxycareninae by China, 1945). Previously, the group was known only from coleopteroid specimens which exhibit the following distinctive features: reduction to complete loss of compound eyes, loss of larval scent gland 3/4, unique structure of lateral scent gland channels 4/5, and branching T-shaped metapleural ostiolar groove (Drake and Davis, 1960). They differ from the Tingidae *s. s.* by the lack of spinosity on head, lack of paranota, the elytralike corium and clavus in coleopteroid forms, lack of areolation in the hemelytra, presence of buccular bridge, long second antennal segment, and normally developed meso-scutellum. We have examined several macropterous specimens, possibly belonging to undescribed genera, from Tabago, Venezuela, and Brazil. They conform in most characters with coleopteroid specimens, but the compound eyes are normally developed. The most important characters of the macropterous forms are: ocelli absent; explanate lateral pronotal margins; posterior pronotal margin not produced posteriad; dorsum heavily punctured; legs long and thin; forewings with a strikingly raised and keel-like media; marginal venation extending to the apex of the membrane forming a sickle-shaped continuation of the corium; and a distinct and well-developed membrane with no cells, free veins, or stub.

Tingidae sensu stricto. A speciose, exclusively phytophagous group, with the recognized subfamilies Cantacaderinae with 2 tribes and the Tinginae with 2 or 3 tribes (Drake and Ruhoff, 1965). The Tingidae *s. s.* is most obviously recognized by the pronotum usually provided with paranota and one or more longitudinal carinae, the areolate forewings with a more or less uniform texture and lacking distinction between corium and membrane, head usually with spines or tubercles, mesoscutellum reduced in size or hidden by the pronotal projection, and small repellent glands distributed over the entire body surface in the larvae (Schultze, in litt.).

Medocostidae. Described by Štys (1967a) from two species of *Medocostes* from western tropical Africa, recently Kerzhner (1989) has recognized only a single species, *M. lestoni.* This group was treated as a tribe of the Velocipedinae by Kerzhner (1971) and as a subfamily of a more inclusive Nabidae by Carayon (1970) and Kerzhner (1981). Our analysis supports Štys's original assignment to family rank, the group being recognized by: absence of the costal fracture, absence of distal corial cells, absence of the buccular bridge, and uniquely by a straight labium with segment 4 longer than segments 2 and 3 combined. *Medocostes* lives on dead trees (Kerzhner, 1989). Sweet (ms) suggested a possible hematophagous habit while Kerzhner (1989) suggested predation on subcorticolous insects. However, the structure of the labium suggests that *Medocostes* may not be predaceous.

Nabidae sensu stricto. We use this family group name to include only the Nabinae and Prostemmatinae of Carayon (1970) and Kerzhner (1981), authors that have used it in a much broader sense to include also the Medocostidae and Velocipedidae. The Nabinae and Prostemmatinae are held together by the structure of the labium, venation of the membrane, and particularly by the presence of fossettes parastigmatiques and Ekblom's organ. Nonetheless, we have treated them as separate entities in our analysis, as part of our effort to recognize a monophyletic Nabidae and because each group possesses unique characters.

Nabinae. Kerzhner (1981), in his World classification, recognized four tribes, viz., Arachnocorini, Carthasini, Gorpini, and Nabini (=Arbelini and Metatropiphorini); these tribes had often been regarded as distinct subfamilies in the Nabidae (e.g., China and Miller, 1959). The group is speciose, of world-wide distribution, and of quite diverse habits. It has usually been recognized on the basis of negative features, such as the lack of scutellar trichobothria (in contrast to the Prostemmatinae), none of the labial segments extremely long or short (in contrast to the Medocostidae and Velocipedidae), and a consistent lack of the costal fracture. Positive features include: the presence in the ground plan of fossettes parastigmatiques on many abdominal segments; the presence of Ekblom's organ associated with 30–40 stiff setae on the apex of the hind tibia of the male (this large setal number being unique to the group); a branching distal sector of R+M in the hind wing (a similar condition occurs also in the Microphysidae and Pentatomomorpha); and the dorsal position of the posterior foramen of the pygophore (Kerzhner, 1981). Many members of the Nabinae diverge from the ground plan of the subfamily; nonetheless, the group has a general habitus of elongate, often nearly parallel-sided, weakly sclerotized insects with a slender, anteriorly projecting head and a relatively long, thin, curving labium.

Prostemmatinae. Many members of this group have a facies similar to the Pachynomidae, although many important features distinguish them. Both groups have apparently 5-segmented antennae. Zrzavý (1991) has shown that only in Pachynomidae are the antennae truly 5-segmented, by virtue of a subdivided pedicel, whereas in Prostemmatinae the prepedicellite is long and conspicuous (see discussion under Pachynomidae and character 6 in Appendix). Early authors often placed the Pachynomidae within the Prostemmatinae, but most recent authors have separated the 2 groups and included the Prostemmatinae within the variously conceived Nabidae. Kerzhner (1981) in his World classification recognized five genera of prostemmatines, placed in two tribes, Prostemmatini (*Alloeorhynchus* Fieber, 1860; *Pagasa* Stål, 1862; *Prostemma* Laporte, 1832) and Phorticini (*Phorticus* Stål, 1860; *Rhamphocoris* Kir-

kaldy, 1901). The family is of world-wide distribution with the greatest diversity in tropical regions. Unique features of the Prostemmatinae are: 1–7 pairs of trichobothria located on the lateral margins of the scutellum (Carayon, 1970) and the caudal or ventral position of the posterior foramen of the pygophore (Kerzhner, 1981). The Prostemmatinae further differ from the Nabinae *s. s.* by having fewer than 10 setae (associated with the presence of Ekblom's organ) on the apex of male hind tibiae (in contrast to the large numbers found in the Nabinae), and by having the fossettes parastigmatiques (if present) uniquely limited to abdominal segment 3. In contrast to the Nabinae which live mostly on vegetation, indiscriminately feeding on soft-bodied insects, the Prostemmatinae are specialized ground-dwelling predators of other heteropterans (Kerzhner, 1981).

Cimicoid families. Most modern authors have recognized 3 families, viz., Anthocoridae, Cimicidae, and Polyctenidae, within this subgroup of cimicomorphans; recently the Plokiophilidae have been added (Carayon, 1974). Nevertheless, Southwood and Leston (1958) noted that the Anthocoridae is not a monophyletic group and in their treatment of the British fauna subsumed its members under a broadly conceived Cimicidae. Carayon, over a period of 3 decades, elucidated the peculiarities of anatomy, reproduction, and life history of the cimicoid complex, offering major summaries of his work in a classification of the Anthocoridae (Carayon, 1972a) and a review of traumatic insemination (Carayon, 1977a). Ford (ms), using the extensive data of Carayon, concluded as did Southwood and Leston, that the Anthocoridae in the traditional sense, and as considered by Carayon (1972a) and Péricart (1972), were paraphyletic. Ford's excellent English language summary of the situation, suggesting that not only Cimicidae, but also Polyctenidae and Plokiophilidae, are subgroups of the classical Anthocoridae. The cladogram and character distributions from Ford's unpublished work were presented by Schuh (1986), who concluded that if we are to accept the easily diagnosed Plokiophilidae, Polyctenidae, and Cimicidae, we must break the classical Anthocoridae into at least 3 families, viz., Lasiochilidae, Lyctocoridae, and Anthocoridae *s. s.* This is the scheme we have followed in our analysis. The recognition of monophyletic groupings within the cimicoid lineage is the only difference with regard to terminal taxa our study and that of Kerzhner (1981).

Lasiochilidae. Lasiochilid genera have been placed in the Anthocoridae by all modern authors. Carayon (1972a) established a separate subfamily to accommodate them. The group is widely distributed but seems to be most diverse in tropical areas, particularly in the New World, and is almost absent from the Palearctic. The general facies of the Lasiochilidae are similar to the Lyctocoridae and Anthocoridae *s. s.,* the males having asymmetrical genitalia with the right paramere greatly reduced, but in contrast to the those groups there is no hemocoelic insemination, and as opposed to other cimicoid groups the spermatheca is in the form of a vermiform gland, as also found in many other non-cimicoid cimicomorphans. The presence of only a single pair of dorsal laterotergites associated with abdominal segments 1 and 2 (all other abdominal segments having a simple tergal plate) is apomorphic for the group (for other characteristics see Carayon, 1972a).

Plokiophilidae. This group of tiny predators was first recognized as distinct family by Carayon (1962a; see also Štys, 1962, 1967b); they were previously treated as members of the Microphysidae (China and Myers, 1928; China, 1953). Currently

two subfamilies—Plokiophilinae (Afrotropical, Madagascan [Štys, unpubl.], and Neo-tropical: *Lipokophila* Štys, 1967; *Plokiophila* China, 1953; *Plokiophiloides* Carayon, 1974) and Embiophilinae (Pantropical: *Embiophila* China, 1953)—are recognized (Carayon, 1974; Ford, ms). Ford (ms) suggested that a distinct subfamily should be established for *Lipokophila*. The monophyly of the group is based on: the structure of the male genitalia with the often elongate tubular pygophore, long symmetrical to weakly asymmetrical slender spiniform parameres, slender partially-coiled phallus, the females with a greatly reduced ovipositor, and the distinctive corial glands on the forewings (Carayon, 1974). In at least some Plokiophilidae the phallus is used in a unique way for symmetrical penetration of the female abdominal dorsum during repeated attempts at copulation (Carayon, 1977a). The life habits of this family are unique among the Cimicoidea, with members of the Embiophilinae living in the webs of Embiidina and those of Plokiophilinae exclusively inhabiting the webs of spiders (China and Myers, 1928; Carayon, 1974; Edgerly, 1987; Eberhard et al., in prep.).

Lyctocoridae. The Lyctocorinae of Carayon (1972a) is an omnibus paraphyletic assemblage. We restrict this group name to the tribe Lyctocorini of Carayon, including only the genus *Lyctocoris* Hahn, 1835 (Ford [ms] included here also the genus *As-temmocoris* Carayon and Usinger, 1965, regarded as Lyctocorinae *incertae sedis* by Carayon [1974]), and place all other members of Carayon's Lyctocorinae in a more restricted Anthocoridae. The group is most speciose in the Northern Hemisphere with a few species known from other regions. The left paramere in the male does not serve as a copulatory organ for penetration of the female body wall, as opposed to the situation in the Polyctenidae, Cimicidae, and most Anthocoridae. Apomorphies include: presence of genital apophysis on sternum 7 of the female, and seminal conceptacles formed by the epithelium of the genital duct in contrast to the Poly-ctenidae, Cimicidae, and Anthocoridae where they are formed by the so called *hemo-chrisme* in the peritoneal sheath of the ovariole.

Anthocoridae. We use the name Anthocoridae in a restricted sense, recognizing a monophyletic, or at least not grossly paraphyletic, group. Ford's (ms) cladogram offered two classificatory alternatives: one, that the Xylocorini and Almeidini are part of the Cimicidae, or that the Cimicidae and Anthocoridae (less Lasiochilidae and Lyctocoridae) should be combined into a single family, a solution more similar to that proposed by Southwood and Leston (1958). The former solution offers greater stability of nomenclature, but a final resolution of this problem will require further study of structural variation in these groups to determine which taxa placed in the Anthocoridae by us should be included in the Cimicidae. We include in the Antho-coridae the following suprageneric taxa recognized by Carayon (1972a): Xylocorini, Almeidini, Dufouriellini (=Cardiastethini), and Scolopini (including Scolopina, and Caliobina) of the Lyctocorinae *sensu* Carayon, and all tribes of the Anthocorinae *sensu* Carayon (Blaptostethini, Anthocorini, Oriini). This is a large and diverse group of world-wide distribution, defined by the presence of seminal conceptacles formed from *hemochrisme* and the absence of characters unique to the Cimicidae. As with the Polyctenidae and Cimicidae, members of the Anthocoridae (except Anthocorini and probably Scolopini) have the left paramere modified into a copulatory organ which penetrates the female body wall (Carayon, 1972a; Péricart, 1972).

Cimicidae. Conceived by most modern authors in a restricted sense and as rec-

ognized here, this group includes only ectoparasites of bats, man, and some birds (e.g., Usinger, 1966). It appears to be most closely related to one of the subgroups of Anthocoridae *s. s.* Ford's (ms) analysis of Carayon's data indicated that the Cimicidae are the sister group of the Xylocorini and possibly Almeidini, here placed in the Anthocoridae (see also comments under Anthocoridae). The Cimicidae were monographed by Usinger (1966), who recognized 6 subfamilies. The group is worldwide in distribution, with the greatest diversity in the tropics. The monophyly of the Cimicidae is documented by: the loss of ocelli, micropterous condition of forewings, temporary parasitism of homeothermous vertebrates associated with hematophagy, dilated anteclypeus, and broadly flattened body. This is the group in which traumatic insemination was first noted and for which the mechanisms of the unusual method of fertilization were first studied in detail (see Carayon in Usinger, 1966).

Polyctenidae. This unusual group of permanent bat ectoparasites has structural modifications presumably associated with its life habits. Giglioli (1864) described *Polyctenes molossus,* the first known species of the family, placing it in the Nycteribiidae (Diptera); ten years later Westwood (1874) placed it in the Anoplura. It was some time before the heteropteran affinities of the group were recognized. Maa (1964) subdivided the family into the Polycteninae (tropical areas of the Old World: *Polyctenes* Giglioli, 1864; *Eoctenes* Kirkaldy, 1906) and Hesperocteninae (pantropical: *Androctenes* Jordan, 1912; *Hesperoctenes* Kirkaldy, 1906; *Hypoctenes* Jordan, 1922). The ventral laterotergites are separate from the mediosternal plate, and the method of traumatic insemination is essentially like that of Cimicidae and Anthocoridae, with the left paramere in the form of a copulatory organ, but penetration is via the metacoxal membrane as opposed to the abdominal wall. Some of the numerous apomorphies include (Ferris and Usinger, 1939): presence of ctenidia, complete absence of compound eyes, labial insertion shifted caudad onto the ventral surface of the head, neotenous aptery, only 3 larval instars (Štys and Davidova-Villímová, 1989), 4-segmented middle and hind tarsi in adults (3-segmented in larvae), and annulated tibiae. Dorsal abdominal scent glands are absent in the larvae of many species (Ferris and Usinger, 1939; pers. obs.), but they were observed by Ferris and Usinger (1945) in larvae of *Hesperoctenes eumops* and 2 unidentified larvae from Brazil. We have observed that at least some polyctenids (e.g., *Eoctenes spasmae*) have a first abdominal sternum developed as a vaguely delimited semisclerotized pilose plate contrasting with the sharply delimited second abdominal sternum. This may represent the neotenous retention of larval morphology and is unique among the Cimicomorpha.

SOURCES OF CHARACTER INFORMATION

We have relied heavily on the published literature as a source of data. References of particular importance were: I. M. Kerzhner's (1981) monograph of the Palearctic Nabidae; numerous papers by J. Carayon dealing with morphology, reproduction, and classification in the Cimicoidea, Prostemmatinae, and Pachynomidae; and papers authored or coauthored by N. T. Davis dealing with comparative morphology of several cimicomorphan families.

Kerzhner's (1981) work represents the most comprehensive attempt to develop a phylogeny for the Cimicomorpha because he dealt with all currently included families, he presented his data in such a fashion that all attributes could be assigned to all

taxa, and his results were in the form of a more or less easily interpretable cladogram. Although we have adopted many of the characters (see characters 0, 3, 5, 16, 17, 19, 21, 22, 29, 30, 36, 37, 39, 41, 43, 49, 50) employed by Kerzhner (1981), we have not used all of them in exactly the same form as published by him, because some, such as labium suited for different types of feeding behavior, could not be satisfactorily interpreted by us, and others (e.g., membrane venation) seemed to be coded in such a way as to introduce some prior conclusion about relationships within the Cimicomorpha. We did not use the position of the hypocostal lamina because its states could not be precisely defined, and the character describing early or late maturation of trophocytes was known from too few taxa. Schuh (1986: caption to fig. 6) misstated Kerzhner's character 3 as "gula absent"; it should have read "buccular bridge absent."

We have used Ford (ms) as an aid in synthesizing the contributions of Carayon on the Cimicoidea *s. s.* Schuh (1986: caption to fig. 8) transcribed in error Ford's character 46, which should have read "double copulatory tubes in female," not in male. Certain aspects of abdominal morphology were suggested as characters in a yet unpublished manuscript by M. H. Sweet.

There are a number of characters or character systems mentioned in the literature which we have not included in our analysis. First, information on the male genitalia in the noncimicoid Cimicomorpha has never been presented in a format suitable for phylogenetic analysis; a modern comparative study is badly needed because the only comprehensive work available is the paper by Singh-Pruthi (1925) which does not meet modern standards. Second, certain information provided by Cobben (1978: tables 5, 6) and later reanalyzed by Schuh (1979), was not documented on a family by family basis for many of the nonreduviid families, and could not be confirmed by us without extensive anatomical studies. And third, although included in the matrix, rotatory and cardinate coxae, as originally recognized by Schiødte (1870), proved impossible to define in an objective way. When included in our computations this character produced variable results, and we have therefore treated it as inactive (see character 18 below).

Information concerning ovariole, testis follicle, and chromosome numbers, as well as other aspects of general internal anatomy have been used by various authors to suggest relationships among certain families of Cimicomorpha and as well as other Heteroptera. We have not included most of these data because in many cases information about them is too scanty and in others intragroup variation is so great that application at the family level is inappropriate.

PHYLOGENETIC METHODS

We would observe that in an ideal situation a higher taxon would be recognized as natural by a character unique to it and the character would be present in an identical form in all constituent subgroups; the more such apomorphies found for a group, the stronger the support for its monophyly. This is indeed the situation for some groups and some characters within the Cimicomorpha. However, the situation is often less clear cut, with many character states showing homoplasy within the group, and seemingly existing in other infraorders of the Heteroptera. Thus, rather than attempting a classical Hennigian analysis in which the monophyly of recognized groups might be based on a few uncontradicted characters, we have assembled as much character information as possible and employed a computer-based phylogenetic

approach in the application of parsimony as an arbiter amongst possible phylogenetic patterns. We do this for two reasons: first, the number of possible phylogenies is reduced to some finite number that have been objectively selected; and second, the most parsimonious solution represents the most economical explanation of the character data for the cladogram and its corresponding hierarchic classification (Farris, 1979, 1983).

Cladograms presented in this study were produced using HENNIG86, an IBM PC based phylogenetics package written by J. S. Farris. It contains a number of parsimony algorithms for the production of cladograms, as well as other utilities for data and cladogram manipulation. Most of our analyses used a combination of the *mh** and *bb** algorithms (heuristic with branch swapping; see Fitzhugh, 1989), intended—but not guaranteed—to find all most-parsimonious solutions, and the results presented were verified as exact solutions using the *ie* algorithm (iterative enumeration, providing all possible most parsimonious solutions).

Cladograms and characters can be readily characterized by 3 attributes: *length*— the number of steps (character-state changes) required to fit the data to the tree; *consistency index* (ci)—the ratio of the minimum number of steps for a character (or all characters) to the actual number of steps on the tree, with a value of 1.00 indicating perfect fit; and *retention index* (ri) (see Fitzhugh, 1989; Farris, 1989)—a measure of synapomorphy, with a value of 1.00 indicating a character all of whose states are consistently distributed on internal nodes of the cladogram and a value of 0.00, indicating a character which has no synapomorphy content (although characters present in a single terminal taxon have a value of 1.00). As mentioned above, we used 2 outgroups, which allowed for the precise determination of the position of the root of the cladograms produced by HENNIG86.

We used the successive approximations weighting approach of Farris (1969; see also Carpenter, 1989) to select among equally parsimonious cladograms derived from the same data on the basis of which were supported by characters of highest consistency. The details of this method as implemented in HENNIG86 are described by Fitzhugh (1989).

Much of the character information included in our study could be coded in a two state format, such that both the primitive and derived conditions represented a distinct structural or functional type, with the condition found in the outgroup being coded as zero (Tables 1, 2). Other character information benefitted from being coded in a multistate format (Fig. 2). In some cases multistate characters could be coded in a linear format with the outgroup condition as zero or as one of the states lying between the end points of the series such that the character branches on the cladogram. Other multistate characters required coding in a more complex branching format. Because HENNIG86 does not directly support complex branching characters we coded characters 19, 21, 22, 34, 37, 43, and 47 in an additive binary format (Farris et al., 1970) shown in Table 2. We present character-state trees for all multistate characters in Figure 2 to assist the reader in understanding the topology of the characters on the cladogram. Mickevich (1982) and Mickevich and Weller (1990) have argued for the inclusion of reciprocal illumination in the analysis and coding of multistate characters. We have adopted much of their approach in an attempt to produce transformation series that allowed for greatest congruence and provide maximum information for all characters being analyzed. Thus, some readers may find

our treatment of certain character information at variance with traditional interpretations found in the heteropterological literature. At various places in the present paper we comment on the consequences of our interpretations.

Those character states which could not be coded (e.g., venational attributes in the Polyctenidae) are indicated by a dash in Tables 1 and 2; those about which we lacked information by a question mark.

Character 18 (coxal types) was treated as inactive, and not included in the final result.
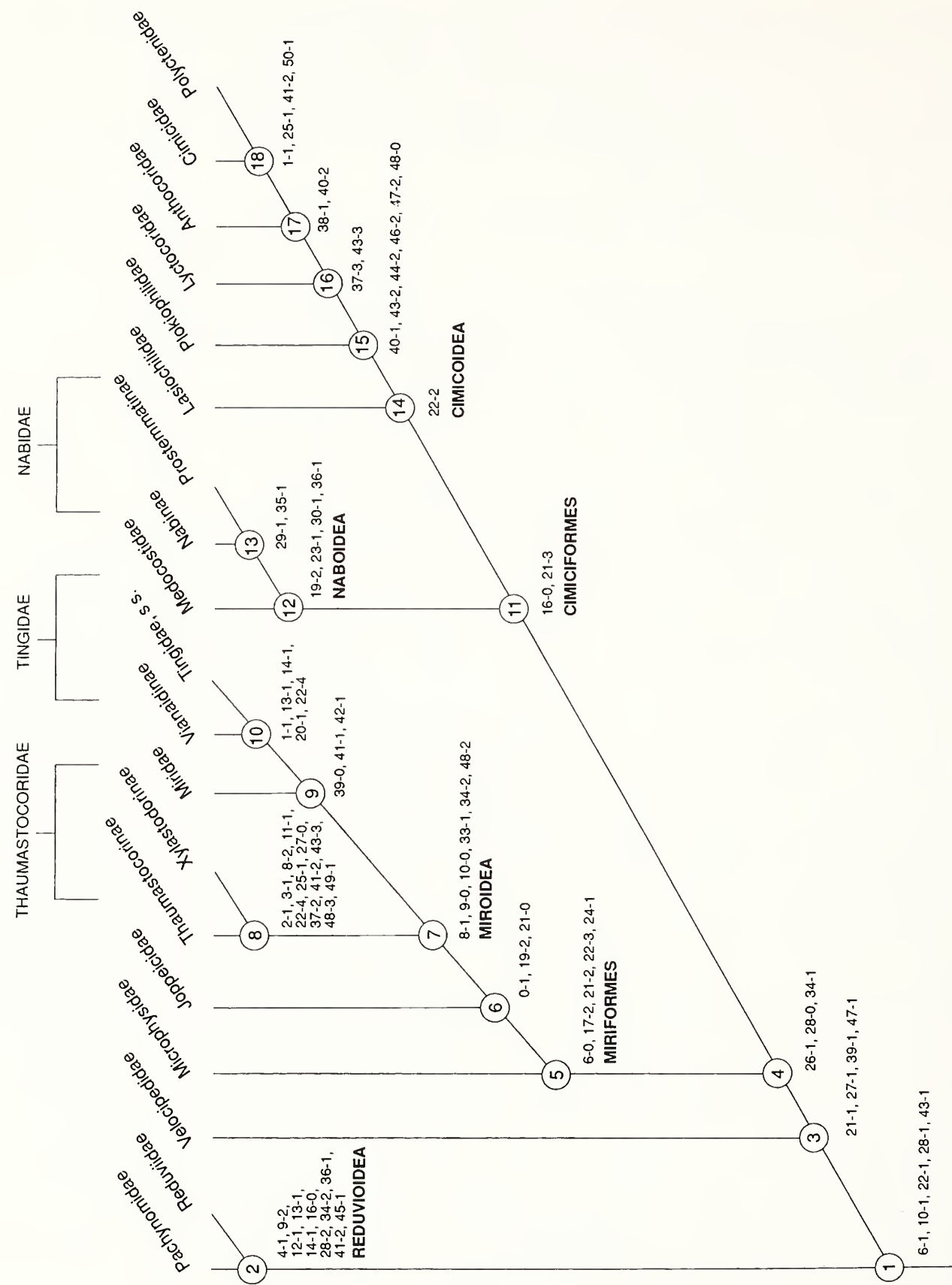
PHYLOGENETIC ANALYSIS

Results of analysis of newly developed data. Character information for this study is presented in the form of a matrix in Tables 1 (linear coding) and 2 (additive binary coding of some multistate characters), with 19 terminal taxa, 2 outgroups, and 51 characters and 127 states; character descriptions and pertinent statistics are given in Table 3; character state trees for multistate characters are given in Figure 2. Explanatory notes and literature references for individual characters are given in the Appendix. In many cases we have resolved ambiguous statements in the literature or clarified variation in family-level groups by examination of specimens. Some characters included in Tables 1, 2 and 3 do not define inclusive groups; nonetheless, we have retained these autapomorphies in the matrix to give our colleagues a more thorough appreciation of the information which we analyzed as well as to give a more precise demonstration of which attributes actually define groups and which do not.

Figure 1 gives the results of our analysis of the data coded in additive binary format as shown in Table 2. This cladogram is one of 2 found and the one to be preferred as determined by successive weighting (length = 156; consistency index = 49; retention index = 68). Specification of the hypothetical ancestor or the Leptopodomorpha as the outgroup made no difference in the results produced by HENNIG86.

Reanalysis of Kerzhner's data. Because part of the impetus for the present paper derived from work of Kerzhner (1981), we sought to determine whether his cladogram (redrawn by us as Fig. 3; see also Schuh, 1986: fig. 6) represented the most parsimonious solution for his data. This was accomplished by constructing a matrix using the distributions as indicated on his published diagram and confirming them by reference to his character descriptions and text discussion. We fitted Kerzhner's data to his own tree, a process which produced a cladogram of a length of 66 steps, with a consistency index of 42 and a retention index of 63. Our computations using the *ie* algorithm of HENNIG86 on the matrix of Kerzhner's data produced 24 trees from which one (Fig. 4) was selected through the use of successive weighting as showing the strongest support from the data (length = 64; consistency index = 43; retention index = 65). Note the difference in topology of the 2 trees (discussed below), and that Kerzhner's tree is slightly longer and has a lower consistency index.

COMPARISON OF CURRENT RESULTS WITH
THOSE OF PREVIOUS AUTHORS

Comparison of our results with those of other authors can be made in two ways: topology of cladograms (monophyletic groups in common) and character support for groupings—whether the same or different—in the schemes being compared.
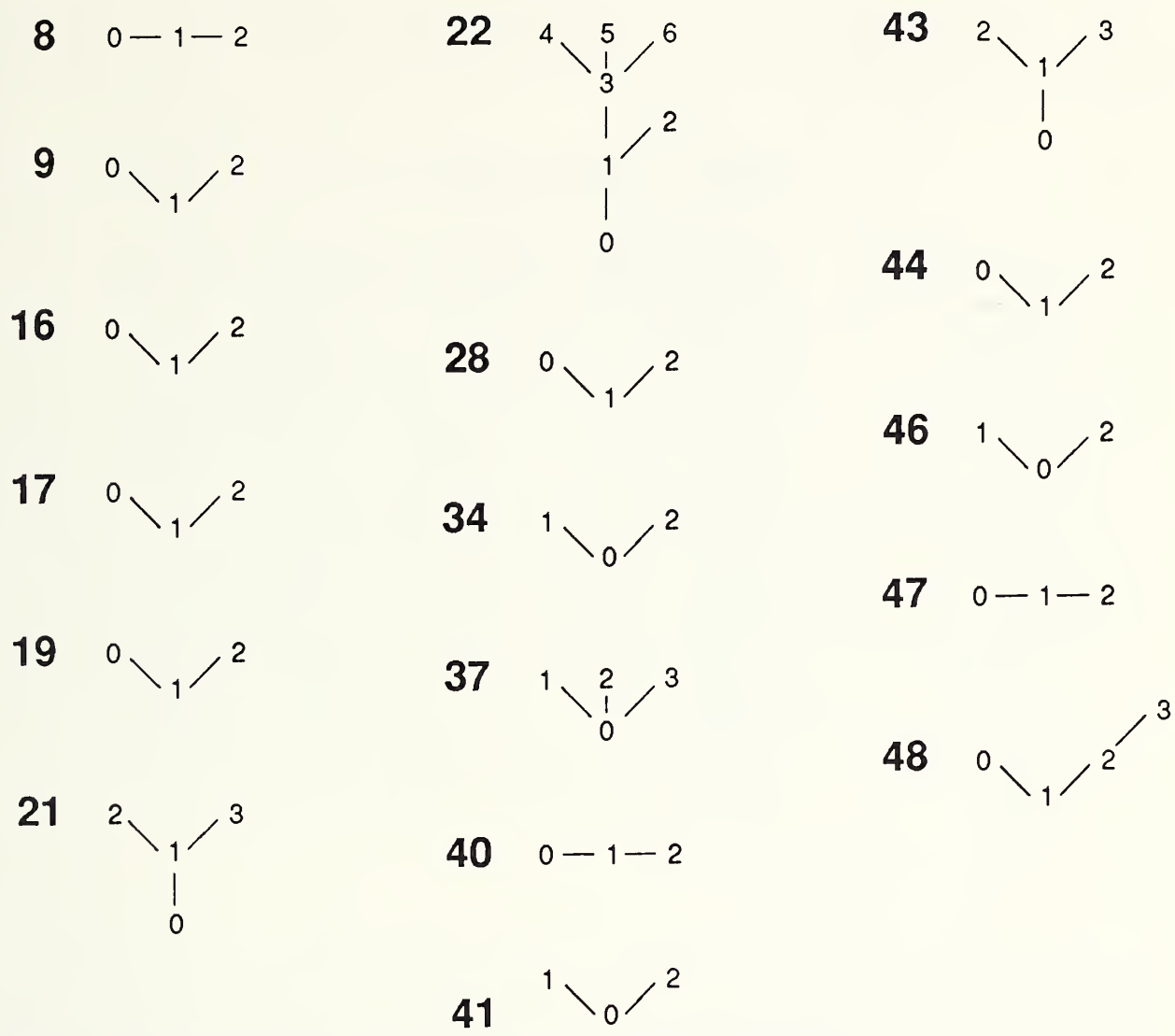
Fig. 2.   Character state trees for multistate characters from Table 1.

Topological comparisons. As mentioned above, 2 explicit schemes of relationships have been proposed for the Cimicomorpha, with some additional classifications implying a phylogenetic scheme. Our results—although based on a very different data set—are in agreement with the results of Schuh (1979), in treating the Pachy-

←

Fig. 1   Cladogram of Cimicomorpha based on 51 characters described in Table 3, with character states for individual taxa listed in Table 1, and computed from the additively binary coded data in Table 2 (character 18 inactive); length = 156, ci = 49, ri = 68. Characters listed by number and state. The following taxa are autapomorphic for the indicated states: Joppeicidae—5-1, 7-1, 13-1, 20-1, 22-5, 34-0, 41-2, 43-2; Lasiochilidae—37-3; Lyctocoridae—30-1; Medocostidae—3-1, 9-0; Microphysidae—12-1, 21-2, 23-1, 25-1, 42-1, 43-3; Miridae—19-0, 21-2, 22-6, 32-1, 37-1, 43-3; Nabinae—26-0, 28-1, 36-0; Pachynomidae—15-1, 19-1, 29-1, 30-1, 43-3, 48-0; Plokiophilidae—12-1, 34-2, 39-0, 41-2, 43-2, 43-2; Polyctenidae—0-1, 3-1, 6-0, 10-0, 12-1, 17-0, 26-0, 28-1; Prostemmatinae—19-1, 23-0, 40-1, 44-0, 46-0; Reduviidae—11-1, 19-2, 42-1, 48-3; Thaumastocorinae—16-2; Tingidae—3-1, 5-1, 43-2, 49-1; Velocipedidae—15-1, 30-1; Vianaidinae—7-1, 31-1, 43-3.

Table 1. Fifty-one characters used for phylogenetic analysis of Cimicomorpha (see Table 2 for additive binary coding, Table 3 for character descriptions, and Fig. 2 for character state trees).

	0000000000 0123456789	1111111111 0123456789	2222222222 0123456789	3333333333 0123456789	4444444444 0123456789	5 0
Leptopodomorpha	0000000001	000?001100	0000001000	0011200000	0000101010	0
ancestor	0000000001	10000011- 0	0000000010	000000000-	0002101010	0
Pachynomidae	0000101002	1011110121	0010000021	1000?01000	0203111000	0
Reduviidae	0000101002	1111100122	0010000020	0000201000	0211111030	0
Velocipedidae	0000001001	100?011110	0110000110	1000200001	000110111?	0
Microphysidae	0000000001	1010001200	0231111100	0000100001	0013101110	0
Joppeicidae	1000010101	1001001222	1050101100	0000000001	0202101110	0
Miridae	1000000010	0000001200	0260101100	0011200100	0111101120	0
Xylastodorinae	1011000020	010?001222	0040111000	0001200201	02?3101131	0
Thaumastocorinae	1011000020	010?002222	0040111000	0001200201	0203101131	0
Vianaidinae	1100000110	0001101222	1040?01100	0101200000	011310112?	0
Tingidae s.s.	1101010010	0001101222	1040101100	0001200000	0112101121	0
Medocostidae	0001001000	100?000112	0311001100	1000?01001	00011011??	0
Nabinae	0000001001	1000000112	0311000111	1000110001	0001101110	0
Prostemmatinae	0000001001	1000000111	0310001101	1000111001	1001000110	0
Lasiochilidae	0000001001	1000000100	0320001100	0000?00301	00?11011?0	0
Plokiophilidae	0000001001	1010000100	0320001100	0000200000	12?2202200	0
Lyctocoridae	0000001001	1000000100	0320001100	1000100301	1003202200	0
Anthocoridae	0000001001	1000000100	0320001100	0000100311	2003202200	0
Cimicidae	0100001001	100000010-	0- - - -11100	0000100311	2203202200	1
Polyctenidae	1101000001	001?00000-	0- - - -10110	0000?00311	22?32022- 0	1

nomidae and Reduviidae as sister groups (an idea first proposed by Carayon, 1950a), and treating that group as the sister group of all remaining Cimicomorpha. This scheme argues against the conclusion of Cobben (1968, 1978) that the two groups are not closely related and also offers additional support for placement of the Reduviidae in the Cimicomorpha, contrary to the view of Cobben.

Certain aspects of our results are at variance with those of Kerzhner (1981), however. The main differences are as follows: Kerzhner's placement of the root (Fig. 3) associated the Miridae and Microphysidae with a lineage containing most of the predatory cimicomorphans, whereas in our scheme they belong to a lineage composed of the phytophagous families and the Joppeicidae; he related the Reduviidae and Pachynomidae as sister groups but treated them as being derived from the "Nabidae" (clearly paraphyletic in Kerzhner's sense), whereas in our scheme they are the sister group of all other cimicomorphans; and, the Velocipedidae are placed more basally in our scheme than in his. The other major difference was his treatment of the Anthocoridae s. l. as if it were a monophyletic group, and the independent divergence of the Plokiophilidae from the "nabid" lineage prior to the divergence of other cimicoids, whereas according to our analysis the Plokiophilidae belong to the cimicoid lineage.

Character support. The following discussion provides some insight into character support for the various internal nodes of the cladogram (Fig. 1).

Node 1. Elsewhere we have listed the modified sperm storage organs and the micropylar structure of the eggs as synapomorphies for the Cimicomorpha. Our

Table 2. Fifty-one characters used for phylogenetic analysis of Cimicomorpha.

	0000000000111111111	1	2	2	2	22222223333	3	33	3	334	4	4	4	4444445
	0123456789012345678	9	0	1	2	34567890123	4	56	7	890	1	2	3	4567890
Leptopod	0000000001000?00110	00	0	000	000000	00010000011	10	00	000	000	00	0	000	1010100
ancestor	0000000000110000011-	00	0	000	000000	00000100000	00	00	000	0-0	00	0	110	1010100
Pachynom	0000101002101111012	01	0	000	100000	00000211000	??	01	000	000	10	0	101	1110000
Reduviid	0000101002111110012	10	0	000	100000	00000200000	10	01	000	000	10	1	100	1110300
Velocipe	0000001001100?01111	00	0	100	100000	00001101000	10	00	000	010	00	0	100	10111?0
Microphy	0000000001101000120	00	0	101	101000	11111000000	01	00	000	010	00	1	101	1011100
Joppeici	1000010101100100122	10	1	000	101001	01011000000	00	00	000	010	10	0	110	1011100
Miridae	1000000010000000120	00	0	101	101100	01011000011	10	00	010	000	01	1	100	1011200
Xylastod	1011000020010?00122	10	0	000	101010	01110000001	10	00	100	010	10	?	101	1011310
Thaumast	1011000020010?00222	10	0	000	101010	01110000001	10	00	100	010	10	0	101	1011310
Vianaidi	1100000110000110122	10	1	000	101010	0?011000101	10	00	000	000	01	1	101	10112?0
Tingidae	1101010010000110122	10	1	000	101010	01011000001	10	00	000	000	01	1	110	1011210
Medocost	0001001000100?00011	10	0	110	100000	10011001000	??	01	000	010	00	0	100	1011??0
Nabinae	0000001001100000011	10	0	110	100000	10001111000	01	10	000	010	00	0	100	1011100
Prostemm	0000001001100000011	01	0	110	100000	00011011000	01	11	000	011	00	0	100	0001100
Lasiochi	0000001001100000010	00	0	110	110000	00011000000	??	00	001	010	00	?	100	1011?00
Plokioph	0000001001101000010	00	0	110	110000	00011000000	10	00	000	001	10	?	110	2022000
Lyctocor	0000001001100000010	00	0	110	110000	00011001000	01	00	001	011	00	0	101	2022000
Anthocor	0000001001100000010	00	0	110	110000	00011000000	01	00	001	112	00	0	101	2022000
Cimicida	0100001001100000010	--	0	---	------	--111000000	01	00	001	112	10	0	101	2022001
Polycten	1101000001001?00000	--	0	---	------	--101100000	??	00	001	112	10	?	101	2022-01

phylogenetic analysis of the group suggests additional synapomorphies. These are: 6-1, presence of the prepedicellite (lost at node 5); and, 10-1, the labium inserted anteriorly on the head (moving to a ventral position at node 7). The presence of the prepedicellite was indicated as possibly synapomorphic for the Cimicomorpha by Zrzavý (1991). The fossula spongiosa (character 16) was thought by Kerzhner (1981) to be synapomorphic for groups contained in our nodes 2 and 11. Other character information in our analysis does not support this interpretation, but rather suggests an independent origin of the fossula spongiosa in the 2 lineages. Characters 22-1 (3–4 cells in the membrane) and 28-1 (spiracles on discrete ventral laterotergites) also support the monophyly of the group, but they show much more variation within the group than the characters mentioned above, and the latter is possibly plesiomorphic, as it occurs widely in the Heteroptera.

Node 2. As indicated in Figure 1, many characters support the monophyly of the Reduviidae + Pachynomidae. Most consistent among these are: 4-1, pedicellar trichobothria; 9-2 structure of the labium; and, 45-1, paired tubular ectodermal pseudospermathecae. Based on their distribution on the cladogram, Brindley's glands (14-1), appear to be of independent origin in the Reduvioidea and Tingidae s. s. + Vianaidinae.

Node 3. This previously unrecognized group receives relatively strong support from 3 characters: 21-1, membrane with more than 1 cell and with a stub on the most anterior cell (modified in descendant lineages); 27-1, abdominal spiracle 1 absent (a condition known also in other infraorders); and 47-1, fertilization in lateral oviducts or ovariole pedicels. Only the Reduvioidea (node 2) have retained abdominal spiracle 1 (appearing as a reevolution in the Thaumastocoridae, node 9; see also discussion

Table 3.   Characters used in the cladistic analysis of the Cimicomorpha. Left margin: character number, number of steps on tree, consistency index, retention index. All characters active except 18. See Figure 2 for character state trees for multistate characters.

Head

0	2	50	83	0—dorsum of head capsule usually with 3 pairs of trichobothrium-like setae, 1—dorsum of head capsule without trichobothrium-like setae
1	2	50	66	0—ocelli present, 1—ocelli absent
2	1	100	100	0—mandibular plates of normal size, 1—mandibular plates greatly enlarged and often distinctly surpassing apex of tylus
3	4	25	25	0—buccular bridge present, 1—buccular bridge absent

Antennae

4	1	100	100	0—pedicel (antennal segment 2) lacking trichobothria, 1—pedicel with between 1 and 20 or more trichobothria
5	2	50	0	0—second antennal segment relatively long, 1—second antennal segment noticeably short
6	3	33	77	0—prepedicellite absent, 1—prepedicellite present
7	2	50	0	0—short, thick, apical seta absent on antennal segment 4, 1—apical seta present on antennal segment 4

Labium

8	2	100	100	0—labial segment 1 short and not strongly dilated to virtually absent, 1—labial segment 1 long and relatively slender, 2—labial segment 1 short but distinctly dilated
9	3	66	83	0—labium straight, appressed to ventral body surface, segments 3 and 4 relatively long, 1—labium at least weakly curving or angularly bent, flexible, elongate, 2—labium short, stout, strikingly curved, and inflexible
10	3	33	66	0—labium inserted on ventral surface of head, 1—labium inserted anteriorly on head

Thorax

11	2	50	50	0—stridulatory prosternal sulcus absent, 1—stridulatory prosternal sulcus present
12	4	25	25	0—metathoracic scent gland grooves present on metapleuron, 1—metathoracic scent gland grooves absent or strongly reduced on metapleuron
13	3	33	50	0—metathoracic scent gland with unpaired reservoirs, 1—metathoracic scent gland with paired reservoirs
14	2	50	66	0—Brindley's gland absent, 1—Brindley's gland present

Abdominal Trichobothria

15	2	50	0	0—abdominal trichobothria absent, 1—abdominal venter with a trichobothrium either side of midline on segments 3–7

Legs

16	3	66	88	0—fossula spongiosa present (at least vestigially) apicoventrally on at least foretibiae, clothed with modified microtrichia, 1—fossula spongiosa absent, 2—tibial appendix present on membrane at apex of tibia, clothed with unmodified hairs
17	2	100	100	0—tarsi 4 segmented, 1—tarsi 3 segmented, 2—tarsi 2 segmented
18 [Inactive]				0—metacoxae cardinate, 1—metacoxae intermediate, 2—metacoxae rotatory

Table 3.   Continued.

Wings

19	6	33	21	0—costal fracture long, delimiting cuneus, 1—costal fracture short, interrupting costal margin of wing, not delimiting a distinct cuneus, 2—costal fracture absent
20	2	50	50	0—R + M in forewing not raised and keel-like, 1—R + M in forewing raised and keel-like
21	4	75	96	0—membrane without a stub, 1—membrane with more than one cell and with a stub on the most anterior cell, 2—membrane with a stub on distal angle of a single cell or pair of cells, 3—membrane with a stub on a vein diverging from corium–membrane boundary or as a separate bulge
22	7	86	94	0—membrane with 4 or 5 long closed cells and no emanating veins, 1—membrane with 3–4 short to long cells (sometimes not closed), not attached to cuneal region, usually with many emanating free veins, or 2 or 3 usually long (rarely short) cells not attached to cuneal region (rarely not closed), and usually with only a few to no free veins emanating from them, and sometimes with one free posterior vein (sometimes branched), 2—membrane with 4–5 free veins, rarely with 1 long closed cell with no emanating veins, 3—membrane with 1 small, strongly sclerotized cell not attached to cuneal region, with a few indistinct emanating veins (with a stub), 4—membrane with no cells (and no stub), either no veins or veins percurrent from corial area not differentiated from membrane, 5—membrane with a short transverse cell and a few free emanating veins (no stub), 6—membrane with 1 or 2 short cells (if 2, the anterior one attached to cuneus), rarely with a few emanating vein-like structures, and with one posterior free vein; stub present on distal angle of cell or cells
23	3	33	0	0—distal sector of R + M in hindwing not branching, 1—distal sector of R + M branching
24	1	100	100	0—m-cu crossvein present in hind wing, 1—m-cu crossvein absent in hindwing

Abdomen

25	3	33	50	0—dorsal laterotergites not fused with mediotergites, 1—dorsal laterotergites fused with mediotergites
26	4	25	40	0—ventral laterotergites visible and not fused with abdominal sternum, 1—ventral laterotergites not visible and fused with abdominal sternum
27	2	50	80	0—abdominal spiracle 1 present, 1—abdominal spiracle 1 absent
28	5	40	50	0—spiracles on ventral plate formed by fusion of sternum and ventral laterotergite, 1—spiracles on discrete ventral laterotergite, 2—spiracles on sternum adjacent to discrete ventral laterotergite
29	2	50	50	0—fossettes parastigmatiques absent, 1—fossettes parastigmatiques present
30	4	25	40	0—apophysis absent internally on abdominal sternum 7 in female, 1—apophysis present internally on abdominal sternum 7 in female
31	1	100	100	0—scent gland present between abdominal terga 3 and 4 in larvae, 1—scent gland absent between abdominal terga 3 and 4 in larvae
32	2	50	0	0—scent gland present between abdominal terga 4 and 5 in larvae, 1—scent gland absent between abdominal terga 4 and 5 in larvae
33	2	50	80	0—scent gland present between abdominal terga 5 and 6 in larvae, 1—scent gland absent between abdominal terga 5 and 6 in larvae

Table 3. Continued.

34	7	28	37	0—scent gland present between abdominal terga 6 and 7 in larvae, 1—scent gland scar present between abdominal terga 6 and 7 in larvae, 2—scent gland absent between abdominal terga 6 and 7 in larvae
35	1	100	100	0—Ekblom's organ absent, 1—Ekblom's organ present
36	3	33	33	0—male abdominal segment 8 normally developed and exposed, 1—male abdominal segment 8 reduced and for the most part telescoped within segment 7

Genitalia and Insemination

37	4	73	92	0—male terminalia symmetrical, 1—male terminalia asymmetrical, mirid type, 2—male terminalia asymmetrical, thaumastocorid type, 3—male terminalia asymmetrical, cimicoid type
38	1	100	100	0—male with noncopulatory paramere, 1—left paramere of male modified into a copulatory organ
39	3	33	66	0—general direction of parameres usually backwards, 1—general direction of parameres forward
40	3	66	85	0—distal portion of phallus in male neither with acus nor situated within paramere, 1—vesica in male with acus, 2—vesica in male membranous and incorporated into paramere
41	6	33	71	0—ovipositor laciniate, valvula I (= gonapophysis I) associated by ramus with valvifer I (= gonocoxite I), 1—ovipositor laciniate, but connection of valvula I with valvifer I lost, 2—ovipositor platelike to reduced
42	3	33	50	0—ventral laterotergite 8 in female free of valvifer I (= gonocoxite I) or incompletely fused with the latter, 1—ventral laterotergite 8 in female fully fused with valvifer I
43	10	30	50	0—spermatheca present and functional, 1—spermatheca transformed into form of a vermiform gland, 2—spermatheca reduced and nonfunctional, 3—spermatheca absent
44	2	100	100	0—spermatolytic nonsyncitial bodies present, 1—spermatolytic bodies absent, 2—spermatolytic syncitial bodies present
45	1	100	100	0—paired ectodermal tubular pseudospermathecae absent, or analogous structures saclike, 1—paired ectodermal tubular pseudospermathecae situated on medial ectodermal portion of female gonoducts
46	2	100	100	0—haemocoelic insemination via puncture of vaginal wall, 1—insemination via normal gonoducts, 2—hemocoelic insemination via puncture of abdominal wall or metacoxal membrane
47	2	100	100	0—fertilization in ectodermal parts of reproductive system, 1—fertilization in lateral oviducts or ovarial pedicels, 2—fertilization in vitellarium

Eggs

| 48 | 6 | 50 | 72 | 0—eggs with no micropyles, 1—eggs with 1 micropyle, 2—eggs with 2 micropyles, 3—eggs with 3 or more micropyles |

Habits

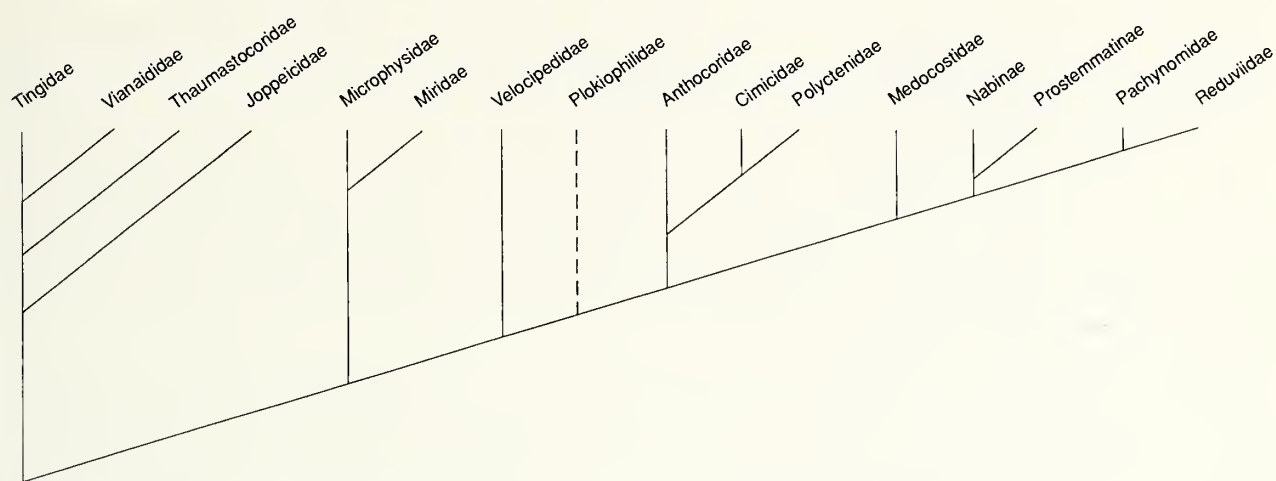| 49 | 2 | 50 | 100 | 0—predaceous, 1—phytophagous |
| 50 | 1 | 100 | 100 | 0—free living, not feeding on vertebrate blood, 1—ectoparasitic, feeding on vertebrate blood |

Fig. 3.   Kerzhner's (1981) cladogram of the Cimicomorpha (redrawn).

of character 27 in the Appendix). Also, only the Reduvioidea retain the plesiomorphic site of fertilization in the ectodermal portions of the female gonoducts, even after the loss of the true spermatheca. In other cimicomorphans, regardless of the method of insemination or in what type of organs (ectodermal or mesodermal origin) the sperm is stored, fertilization always occurs in the mesodermal portions of the female gonoducts or even in the vitellarium, as documented or inferred from anatomical structure in numerous papers by Carayon (e.g., 1954, 1977a).

Velocipedidae. The absence of the fossula spongiosa in this apparently predatory group is something of an enigma to us. Nonetheless, close examination of a number of species, with both males and females represented, revealed no evidence of the structure.

Node 4. This grouping receives its strongest support from characters 26-1, the fusion of the ventral laterotergites with the sternal plate (ventral laterotergites being present only in the Nabinae and Polyctenidae, and possibly indicated in the Prostemmatinae: Phorticini) and 28-0, the location of spiracles 2-8 on that plate (excluding the above mentioned taxa). Both attributes show considerable variation within the

Fig. 4.   Most parsimonious cladogram based on Kerzhner's (1981) data.

Heteroptera, but are highly consistent within the Cimicomorpha. Character 34-1, presence of scent gland scars on larval abdominal segments 6–7 is probably a remnant of a once present gland.

Node 5. The loss or reduction of a number of features serve to characterize this lineage. These include: absence of the prepedicellite (6-0); reduction of number of cells in the membrane (22, several states); and, absence of m-cu in hind wing (24-1). All members of the clade except most Miridae have 2-segmented tarsi (17-2) (see Character Discussion below).

Node 6. Inclusion of the Joppeicidae at this node is somewhat problematic, in that it possesses mostly autapomorphies as well as having certain primitive characteristics (e.g., retention of spermatheca, larval gland 6/7) that do not occur in the remaining members of this lineage. Nonetheless, lack of cephalic trichobothria (0-1), absence of the costal fracture (19-2), and absence of the stub on the membrane (21-0) argue for the monophyly of the group (see Character Discussion below).

Node 7. This node groups together those families of Cimicomorpha most of whose members are phytophagous. They all have a labium of similar structure to that found in the Pentatomomorpha (8-1, 9-0, 10-0) (which has been further modified in the Thaumastocoridae in a way also found in some Dipsocoromorpha), but our analysis suggests clearly that the similarity of structure in the labium in these last two groups is the result of convergence. There is also considerable consistency in the absence of larval scent glands between abdominal segments 5-6 and 6-7 (33-1, 34-2) and presence of 2 micropyles on the egg (48-2; secondarily modified in the Thaumastocoridae).

Node 8. Although the two subgroups of Thaumastocoridae recognized here have been associated with one another by most modern authors (a grouping with substantial character support in our analysis), their position within the Heteroptera, and more specifically, the Cimicomorpha, has been thought problematic in the minds of some authors (e.g., Cobben, 1978). Nonetheless, as noted above, there are a number of characters which unite the Thaumastocoridae with the Miroidea of Drake and Davis (1960). The thaumastocorid micropylar type was found to be unique by Cobben (1968), but nevertheless appears to be derived from the mirid-tingid type (2 micropyles) as already noted. The phylogenetic analysis suggests the tibial appendix found in the Thaumastocorinae (character 16-2) is not homologous with the fossula spongiosa of other cimicomorphans, and we have so coded it.

Node 9. The Miridae have been associated with the Tingidae s. l. by some authors (e.g., Drake and Davis, 1960). Although both groups have many characters unique to them, there is support for a sister group relationship, particularly in the structure of the ovipositor (41-1; 42-1).

Miridae. Among those characters listed in the caption to Figure 1 as diagnostic for the Miridae, the cladogram suggests that several have arisen secondarily. The presence of 1 or 2 cells in the membrane (22-6) appears to be derived from the condition of having no cells. The stub (21-2), which is readily observed on the distal angle of the cells in many Miridae, like the membrane venation itself, appears to have arisen from the stubless condition; the stub is present elsewhere in the Miriformes only in the Microphysidae. The Miridae are coded as having 2-segmented tarsi (17-2), because many of its most primitive members—Isometopinae, Psallopinae, some Cylapinae—have that condition, whereas the majority of all others have 3-segmented tarsi. See also Character Discussion below.

Node 10. The Tingidae *s. s.* and Vianaidinae appear as sister groups in our analysis, which is in agreement with the conclusions Drake and Davis (1960) and Carayon (1962b). Character state 14-1, presence of Brindley's glands, shared with the Reduvioidea, suggests that the similar appearing structures in the two groups are not homologous.

Node 11. This grouping of Medocostidae + Nabidae + Cimicoidea is supported by the presence of the fossula spongiosa (16-0) and the distinctive structure and location of the stub (21-3). We assume that in the Velocipedidae and Microphysidae the stub has remained associated with a cell on the membrane, while it has been transferred onto the vein forming the corium–membrane boundary in the taxa grouped under this node. Carayon (1950a, and elsewhere), on the basis of anatomical characters, noted what he believed to be a close relationship between the Nabidae and Cimicoidea *s. s.* as opposed to a relationship between the Nabidae and Reduviidae. Clearly, our results support his contention.

Node 12. Character 19 (condition of the costal fracture), 23-1 (distal sector of R+M branching), and 30-1 (internal apophysis on abdominal segment 7 of female) all are variable within this group and/or occur in other cimicomorphan taxa. They nonetheless support a close relationship among these 3 groups. Carayon (1970) and Kerzhner (1981) included the Medocostidae (and Velocipedidae) within the Nabidae. Kerzhner (1981) supported this by 3 "synapomorphies," viz., 1) presence of the fossula spongiosa (a synapomorphy of the Cimiciformes), 2) loss of live veins on the membrane jointly with the presence of a "stub" (actually synapomorphic at node 11, including also the Cimicoidea), and 3) presence of taenidia (sclerotized supporting rings) in the seminal duct between the basal apparatus of the phallus and the endosoma (Carayon, 1970: fig. 29; Kerzhner, 1981: figs. 59v, 63). Only the last character may be synapomorphic for node 12, but there is no comprehensive comparative morphological study available and we have therefore not included it in our analysis. In view of the relatively weak character support for this grouping we follow Štys (1967a) and treat *Medocostes* as belonging to a distinct family.

Node 13. The two subgroups of Nabidae (with their rather different facies) are held together by their possession of fossettes parastigmatiques (29-1) and Ekblom's organ (35-1), the former attribute also apparently occurring in the Pachynomidae, although our analysis suggests that the structure in that family is of a different origin based on its distribution in our cladogram.

Node 14. Although the facies of taxa included at this node are quite similar (with the exception of the Polyctenidae), character support is somewhat ambiguous because of the variant membrane venation (character 22) and the essentially symmetrical male genitalia in the Plokiophilidae. In our view, the simplest explanation is that the form of the left paramere (37-3) in the Lasiochilidae is not homologous with that found in the Lyctocoridae, Anthocoridae, Cimicidae, and Polyctenidae. Certainly, our analysis strongly suggests asymmetrical male genitalia have arisen several times in the Cimicomorpha.

Node 15. The studies of Carayon, as synthesized by Ford (ms) offer strong support for the taxa included at this node from characters in the male and female genitalia and reproductive systems and the eggs (40-1, 43-2, 44-2, 46-2, 47-2, 48-0).

Node 16. The asymmetrical male genitalia (37-3), and spermatheca absent (43-3) suggest that all taxa at node 16 form a monophyletic group.

Node 17. The structure of the left paramere, in the form of a copulatory organ (38-1) and the membranous vesica incorporated into that paramere (40-2) support grouping the Anthocoridae, Cimicidae, and Polyctenidae. The relationships of the Cimicidae are strongly suggested as with the Xylocorini; however, the Polyctenidae, with their grossly modified structure, assume a much less clear-cut position, outside of the fact that their male and female genitalia clearly associate them with the Anthocoridae and Cimicidae.

Node 18. Although 4 attributes indicate that the Cimicidae + Polyctenidae form a monophyletic unit, we place little credence in this result. The Polyctenidae possesses some seemingly plesiomorphic characters (such as distinct ventral laterotergites [26-0, 28-1]; well developed first labial segment; and presence of the first abdominal sternum, a feature unique in the Cimicomorpha). We regard these attributes as reversals or possibly associated with a neotenous nature of this family; the method of traumatic insemination in the Polyctenidae differs from that of the other cimicoid families and has been regarded by Carayon (1977a) as plesiomorphic.

DISCUSSION OF SELECTED CHARACTERS

Ocelli. Absence of ocelli is often associated with brachyptery in the Heteroptera. Even though certain families lack ocelli on a consistent basis (Tingidae, most Miridae, Pyrrhocoridae, Largidae, and most nepomorphan families), occasionally ocelli are absent in genera perfectly capable of flight, but which nonetheless belong to families which almost consistently possess the organs (e.g., *Camptocera* and *Lipostemmata* in the rhyparochromine Lygaeidae). The loss of ocelli in the Cimicomorpha is a synapomorphy uniting the Tingidae *s. s.* with the Vianaidinae, and the Cimicidae with the Polyctenidae (a grouping of doubtful validity, none of whose members can fly). Ocelli are occasionally lacking in some members of other families such as Reduviidae, Anthocoridae, and female Microphysidae, but consistently only in the Miridae other than the Isometopinae. Thus, the loss of ocelli appears to be a character of little phylogenetic significance, at least within the Cimicomorpha, though their independent loss in the Tingidae and non-isometopine Miridae is noteworthy, and we find no evidence to suggest that those groups, *inter se,* are not monophyletic.

Labial segmentation. Discussions in the literature about the labium have revolved primarily around whether or not segment 1 is present or not. Our observations and analysis suggest that much of such discussion is irrelevant because the degree of development in segment 1 is highly variable even within individual families in the Cimicomorpha. For example, it is greatly reduced to absent in most, but not all Reduviidae, and in many, but by no means all, Cimicoidea (e.g., present in the Polyctenidae). The more fundamental distinction seems to be whether labial segment 1 takes on a form similar to that found in the Miridae and other predominantly phytophagous lineages (elongate and somewhat flared distally), or whether it is of the form found in the predators (usually relatively short to almost absent and of nearly uniform diameter over its entire length). Variation similar to that found in the Cimicomorpha is also found in the Leptopodomorpha, and indeed other higher groups such as the Dipsocoromorpha and Nepomorpha show substantial variation in labial length and the proportional lengths of the segments.

Costal fracture. The absence or presence (and degree of development) of the costal fracture is problematic in that no matter how the transformation stages are coded, the character is always homoplasious on the cladogram. We have regarded the long costal fracture as plesiomorphic in the Cimicomorpha because it is usually long in the Saldidae. The costal fracture is present in this condition in some Pachynomidae (a short fracture being an apparent reduction), Velocipedidae, Microphysidae, and Cimicoidea, but is lost elsewhere, notably in the Reduviidae, and groups contained in nodes 6 (Joppeicidae and Miroidea) and 12 (Naboidea) of Figure 1. However, the costal fracture must be re-evolved in the Miridae (as a long fracture which has been independently lost in a few genera) and Prostemmatinae, respectively. Two less parsimonious explanations are that the presence of the costal fracture always represents a primitive condition and that losses are more frequent than suggested on the cladogram; or, that the costal fracture is a character not belonging to the cimicomorphan (and possibly heteropteran) ground plan, and that it has evolved independently in all of those groups that possess it. It appears that a re-examination of the homology of the costal fracture in the entire Heteroptera will be necessary to further clarify the situation.

Membrane venation and stub. Kerzhner's treatment of the Reduvioidea as closely related to the Nabinae and Prostemmatinae, derived largely from his view that the membrane venation in these groups consists only of "dead" veins. In our earliest attempts at coding characters of wing venation, we accepted Kerzhner's theory of evolution of veins in the membrane exactly as he presented it. This interpretation yielded results in which attributes of membrane venation were not congruent with other characters. We therefore reexamined and recoded characters pertaining to membrane venation, treating cell forming veins as homologous (Table 1, character 22), an approach which produced a much more stable result and much greater character congruence. Our parsimony analysis suggests that the membrane venation has arisen *de novo* in the Miridae after having been lost at node 6 in Figure 1.

The stub (coded as character 21, separately from the free and cell forming veins of the membrane) emerged from our analysis as an important group defining character, although it previously had been incorporated in systematic studies of the Heteroptera only by Kerzhner (1981). The pattern of occurence of the stub is most complicated in the Miriformes and follows a pattern of occurence identical to that of the membrane veins themselves. Our parsimony analysis suggests that the stub is in the ground plan of that group and that it has reevolved in the Miridae. We suggest that additional enquiry will probably support the theory of multiple loss, because the absence of the stub within the Miriformes is restricted to those groups in which membrane venation is greatly reduced or completely wanting, viz., Joppeicidae, Thaumastocoridae, and Tingidae *s. l.*

Fossula spongiosa. Kerzhner (1981) treated the fossula spongiosa, a character unique to the Cimicomorpha, as a synapomorphy for the Reduvioidea and taxa contained in our node 11. Our parsimony analysis suggests that the structure has evolved independently in the Reduvioidea and Cimiciformes, rather than having been lost twice independently (in the Velocipedidae and the taxa contained in node 5) as would be required if it were interpreted as synapomorphic for the Cimicomorpha on the cladogram in Figure 1. Detailed morphological comparison of the fine structure of the fossula spongiosa in the Reduvioidea and the Cimiciformes should be conducted

to provide additional information supporting one of these alternatives.[1] The tibial appendix in the Thaumastocorinae seems rather obviously to be an organ developed *de novo* and not homologous with the fossula spongiosa found in other cimicomorphans.

Tarsal segmentation. The literature on the Cimicomorpha is filled with arguments concerning whether number of tarsal segments is diagnostic for higher taxa or placement of various "annectant" genera. Reading such comments one might conclude that reduced tarsal segmentation is simply an autapomorphous condition in a few families. However, our analysis supports the idea of 2-segmented tarsi as a synapomorphy for a large clade (node 5), with substantial support from other characters. Not only might this result render much previous discussion moot, but it also has implications for the condition of the tarsus in the Miridae. If, as is generally assumed, the Isometopinae are the sister group of all other Miridae, then the 2-segmented tarsi may be part of the ground plan of the group. Indeed, several apparently primitive non-isometopine genera of Miridae, e.g., *Peritropis* Uhler and *Psallops* Usinger also have 2-segmented tarsi.

Abdominal spiracle 1. The first abdominal spiracle appears to have been re-evolved in the Thaumastocoridae, based on the position of the group on the cladogram, and the fact that the structure occurs elsewhere in the Cimicomorpha only in the Reduvioidea. To assume that abdominal spiracle 1 has been retained in the thaumastocorids would require losing it 5 times independently in other taxa. We might assume that in the stem group for node 3 the genetic information regulating the development of the spiracle has been blocked, but never fully lost.

Vermiform gland. Kerzhner's (1981) placement of the root in his cladogram was based strongly on the presumption that the possession of a vermiform gland (character 43-1) is synapomorphic for cimicomorphans that possess the structure (and those which apparently have lost it secondarily, i.e., Pachynomidae, Microphysidae, and most Cimicoidea). Our interpretation suggests rather that the vermiform gland is synapomorphic for all Cimicomorpha and that it has been modified or lost in all groups that do not possess it. What seems clear is that our understanding of homology with regard to transformation of the functional spermatheca is in need of further

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[1] Three attributes, the fossula spongiosa, stub on the forewing membrane, and general venation of the forewing membrane, all appear to be independently evolved in 2 cimicomorphan lineages—at least according to our parsimony analysis. This result exists in spite of the fact that we have coded all characters in such a way as to show maximum congruence on the cladogram—at least within the limits of our ability to understand homology. The multiple evolution of complex structures has been deemed by many authors a less satisfactory explanation of character evolution than multiple loss, even though one or more additional steps may be required on the cladogram. In the case of the three attributes mentioned above, we are also inclined towards multiple loss as the preferred explanation, by virtue of the fact that relatively complex characters need not appear more than once in an apparently identical form. Nonetheless, other factors, such as a sample for the Joppeicidae with no variation, may influence our ability to correctly determine homology; indeed the Joppeicidae are one of the most difficult groups to place (have the relatively weakest character support) in our scheme. Detailed structural analysis may help to determine whether all of our homology statements are correct. Corroboration or rejection of the phylogenetic theory presented in Figure 1 will require additional character information, possibly from molecular data.

study in the Cimicomorpha. Particularly puzzling is the occurrence of a "vestigial" spermatheca not transformed into a vermiform gland in such distantly related groups as Joppeicidae, Tingidae (Cantacaderinae), and Plokiophilidae, all the more so when one notes that these groups are placed relatively high on the cladogram.

Some other striking similarities of apparently independent origin might be mentioned, as for example the presence of Brindley's glands in the Reduvioidea and Tingidae. However striking some of these resemblances, they represent only homoplasies in individual characters, and more thorough morphological and developmental investigations could (and should, if we are right), reveal that similarities in these and other cases are superficial rather than the result of homology.

CLASSIFICATION OF THE CIMICOMORPHA

The last well documented effort at a comprehensive suprafamilial classification of the Cimicomorpha was that of Reuter (1910); yet, his effort now has many limitations, because of a revised diagnosis and consequent altered composition of the group. Štys and Kerzhner (1975) provided a formal classification of superfamilies, but without character documentation; we do not attempt here to list or discuss all of the diverse superfamilial concepts that exist in the literature. Schuh (1986) listed only two higher categories that could be recognized more or less consistently: Reduvioidea and Cimicoidea *s. s.*, with all other families being treated as *incertae sedis.* Carayon (1977a, b, 1984) and Péricart (1983) recognized the Reduvioidea and Cimicoidea, the latter taxon including all non-reduvioid cimicomorphans. Carayon subdivided his very broadly conceived Cimicoidea into two series, Miriformes and Cimiciformes (names proposed by Reuter [1910], for groups of a somewhat different conception); these two groups correspond to clades recognized in our analysis, with the exception of the Velocipedidae and Thaumastocoridae, and we have therefore recognized them in the following formal sequenced classification (Nelson, 1973):

Cimicomorpha
  Reduvioidea
    Pachynomidae
    Reduviidae
  Velocipedoidea
    Velocipedidae
  Miriformes
    Microphysoidea
      Microphysidae
    Joppeicoidea
      Joppeicidae
    Miroidea
      Thaumastocoridae
      Miridae
      Tingidae
  Cimiciformes
    Naboidea
      Medocostidae
      Nabidae

Cimicoidea
  Lasiochilidae
  Plokiophilidae
  Lyctocoridae
  Anthocoridae
  Cimicidae
  Polyctenidae

The Reduvioidea have been recognized by many authors, and our analysis supports the group as well founded. We continue the formal use of this name.

The lineage including the Velocipedidae and all remaining Cimicomorpha has been recognized explicitly by Péricart (1983) and implicitly by Carayon (1977a, b, 1984). We emphasize that the inclusion of the Velocipedidae in the Nabidae, as done by several modern authors (Carayon, 1970; Kerzhner, 1971, 1981) obscures the true relationships of the group. Kerzhner (1981) found support for his admitted paraphyletic and broadly conceived Nabidae (including Velocipedidae and Medocostidae) in an essentially similar phallus (all elements of the basal apparatus fused in a ring, the latter fused with the proximally membranous phallotheca, and the endosoma membranous and not subdivided into a conjunctiva and vesica). This type of phallus may actually be synapomorphic for all Cimicomorpha, or at least non-reduvioid cimicomorphans, and in the absence of a more detailed comparative study, we cannot accept it as merely a "nabid" synapomorphy. Although Kerzhner's (1981) classification of the Nabidae is not accepted here, he clearly recognized the relatively primitive phylogenetic position of the Velocipedidae within the Cimicomorpha, as can be seen in his cladogram. We place the family in a distinct superfamily, Velocipedoidea.

For the microphysid-mirid lineage, we use the existing name Miriformes as applied by Carayon. Classical authors, such as Reuter and McAtee and Malloch, often included the Microphysidae within the Anthocoridae *s. l.* When the Plokiophilidae were first discovered they were placed in the Microphysidae because the known members had two-segmented tarsi. Improved knowledge of genitalic structure in the true cimicoids and the Microphysidae made it clear that no such close relationships existed. A relationship between the Microphysidae and Miridae has been suggested by some authors (e.g., China, 1933, 1955; Štys, 1962; Kerzhner, 1981), and our results suggest that this theory has merit over the microphysid-cimicoid theory. We place the Microphysidae within the superfamily Microphysoidea, to our knowledge for the first time.

The position of the Joppeicidae has always been the subject of dispute. The group has many unique characters, and is placed in the Miriformes with difficulty because of the structure of the labium and its insertion anteriorly on the head. Davis and Usinger (1970) suggested that *Joppeicus* was related to the Tingidae, a similar position being advocated by Kerzhner (1981). Likewise, Carayon (1977a, b, 1984) and Péricart (1983) explicitly related the Joppeicidae to the Tingidae, including also the Miridae and Microphysidae, but made no mention of the Thaumastocoridae. We treat the Joppeicidae as the single family within the Joppeicoidea, as already done by Štys and Kerzhner (1975).

Drake and Davis (1960) used the name Miroidea to include the Tingidae *s. l.* and

the Miridae. Our results support their theory, including the treatment of the Vianaidinae as a subfamily of the Tingidae. However, we use Miroidea in a broader sense, to include also the Thaumastocoridae.

For the nabid–cimicoid lineage we use name Cimiciformes as construed by Carayon (1977a, b, 1984), but excluding the Velocipedidae. We recognize two superfamilies, Naboidea and Cimicoidea *s. s.*

Naboidea. We recognize the Nabidae as including only the Nabinae and Prostemmatinae. The Medocostidae, sometimes included in the Nabidae (e.g., Kerzhner, 1981), always grouped with the Nabidae in our analyses, but because of the unusual combination of attributes, we treat the group as a distinct family.

Cimicoidea. We use this term in the sense of Ford (ms), to include only the Plokiophilidae, Cimicidae, Polyctenidae, and those taxa placed in the traditional Anthocoridae (Lasiochilidae, Lyctocoridae, and Anthocoridae *s. s.*).

In preparing the present classification of the Cimicomorpha the following taxa presented the question of appropriate rank: Isometopinae + Miridae; Thaumastocorinae + Xylastodorinae; Nabinae + Prostemmatinae; Cimicidae + Anthocoridae; and Phymatinae (and related subfamilies) + Reduviidae.

Unfortunately, the process of classification offers no obvious rules for determining the ranks of taxa. At a minimum we recognized monophyletic groups. Beyond that, we have grouped at the family level units which are monophyletic and also satisfied one or more of the following criteria: the rank was in accord with that assigned by recent authorities in the group; the range of morphological variation was less within the group than between it and its sister group; long recognized nomenclature was retained while still satisfying other criteria; and the taxon had been traditionally recognized.

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APPENDIX

EXPLANATION OF CHARACTERS AND
DISCUSSION OF THEIR INTERPRETATION

Head

0. Cephalic trichobothria are widely distributed in the Heteroptera, and appear to be part of the ground plan for the order, at least at the level of Euheteroptera and possibly also including Enicocephalomorpha. Andersen (1982) proposed the deep pitlike bothrium as a synapomorphy in the Gerromorpha. In non-gerromorphan Heteroptera there is often little difference other than length and constant position to distinguish the trichobothrium-like setae from many other setae on the head, but their loss in many groups has been interpreted as a synapomorphy by Kerzhner (1981), and when treated as such does seem to be congruent with the distribution of other characters in the Cimicomorpha (see also Schuh, 1979). Not all members of those groups for which cephalic trichobothria are indicated as present actually have the structures, and some taxa for which they are indicated as lost, appear to possess them.

1. Ocelli are coded as present in the Miridae because of their existence in the Isometopinae, the putative sister group of all other Miridae (Schuh, 1974, 1976).

2. We adopt the term mandibular plate (=juga, paraclypeus) in accordance with current morphological usage. In most cimicomorphans this structure is normally developed, whereas it is generally enlarged in the Thaumastocorinae and Xylastodorinae (see figures in Drake and Slater [1957], and Slater and Schuh [1990]).

3. The buccular bridge is a transverse rampartlike structure formed by the bucculae, situated at the anterior margin of the gula and caudad of the base of the labium. It occurs in most predaceous Heteroptera, but it is often absent in phytophagous groups with long bucculae. The structure has been recognized, and its distribution in the

Cimicomorpha checked, by Štys (unpubl.) during his comparative study of the *Medocostes*. Presence or absence of the buccular bridge was used as a character by Kerzhner (1981). We have done additional checking for the structure in the Thaumastocorinae (absent with the possible exception of *Thaumastocoris*), Xylastodorinae (absent), and Polyctenidae (absent), and Vianaidinae (present).

Antenna

4. Lent and Wygodzinsky (1979) documented the occurrence of pedicellar trichobothria in the antennae of Triatominae (Reduviidae). Wygodzinsky and Lodhi (1990) provided detailed information of their distribution in most reduviid subgroups as well as in the Pachynomidae. We note that a few members of these groups do not possess the structures. Zrzavý (1990) summarized the occurrence of antennal trichobothria in all Heteroptera.

5. Kerzhner (1981) recognized two character states relative to the length of antennal segments 1 and 2: segments 1 and 2 short, or at least segment 2 long. Our analysis suggests that the actual character information concerns the length of segment 2. A short second segment is always combined with a short first segment in Joppeicidae and in most Tingidae *s. s.*, although some Tinginae may have a very long first segment. Contrary to Kerzhner, segment 2 is always long in the Thaumastocorinae and in *Xylastodoris*; only in *Discocoris* (Xylastodorinae), is segment 2 very short. Thus, we coded both Thaumastocorinae and Xylastodorinae as having segment 2 long, as this appears to be the ground plan condition.

6. The distribution of the prepedicellite is based on the work of Zrzavý (1991). The prepedicellite is a secondary segment formed by the separation of the base of the pedicel; it is usually small and ringlike, but sometimes conspicuously long, as in the Prostemmatinae. Some families exhibit some degree of variation; of those coded as lacking the prepedicellite some Miridae (Termatophylini) possess it, while of those coded as having the structure, it is actually absent in many Cimicidae (Cimicinae) and Reduviidae.

7. The distribution of the apical antennal seta is based on the work of Zrzavý (1991).

Labium

8. The first labial segment is truly elongate in the Tingidae *s. s.*, Vianaidinae, and Miridae only (Fig. 5F); it is abbreviated and distinctly dilated in the Thaumastocoridae and Xylastodorinae (less strongly so in *Xylastodoris*) (Drake and Slater, 1957: fig. 7), in a manner similar to that found in many Schizopteridae. In all other families of Cimicomorpha labial segment 1 is noticeably abbreviated (Fig. 5D), and in some taxa hidden between the bucculae (Fig. 5G), or it may be reduced to a ring or be virtually absent (Fig. 5E); we have combined all of these conditions under state 1 because many transitional conditions occur and because the situation in some families is quite diverse. Labial segment 1 is well developed in the Palearctic genera of Microphysidae, but strongly abbreviated in the American genera of the family. It is well developed and externally easily visible in the Nabinae, Prostemmatinae, Pachynomidae, and Reduviidae, Centrocneminae (Miller, 1955, 1956a). It is strongly abbreviated and hidden between the bucculae in the Velocipedidae and Medocostidae, and is reduced to a ring or virtually absent in the other Reduviidae, Joppeicidae,
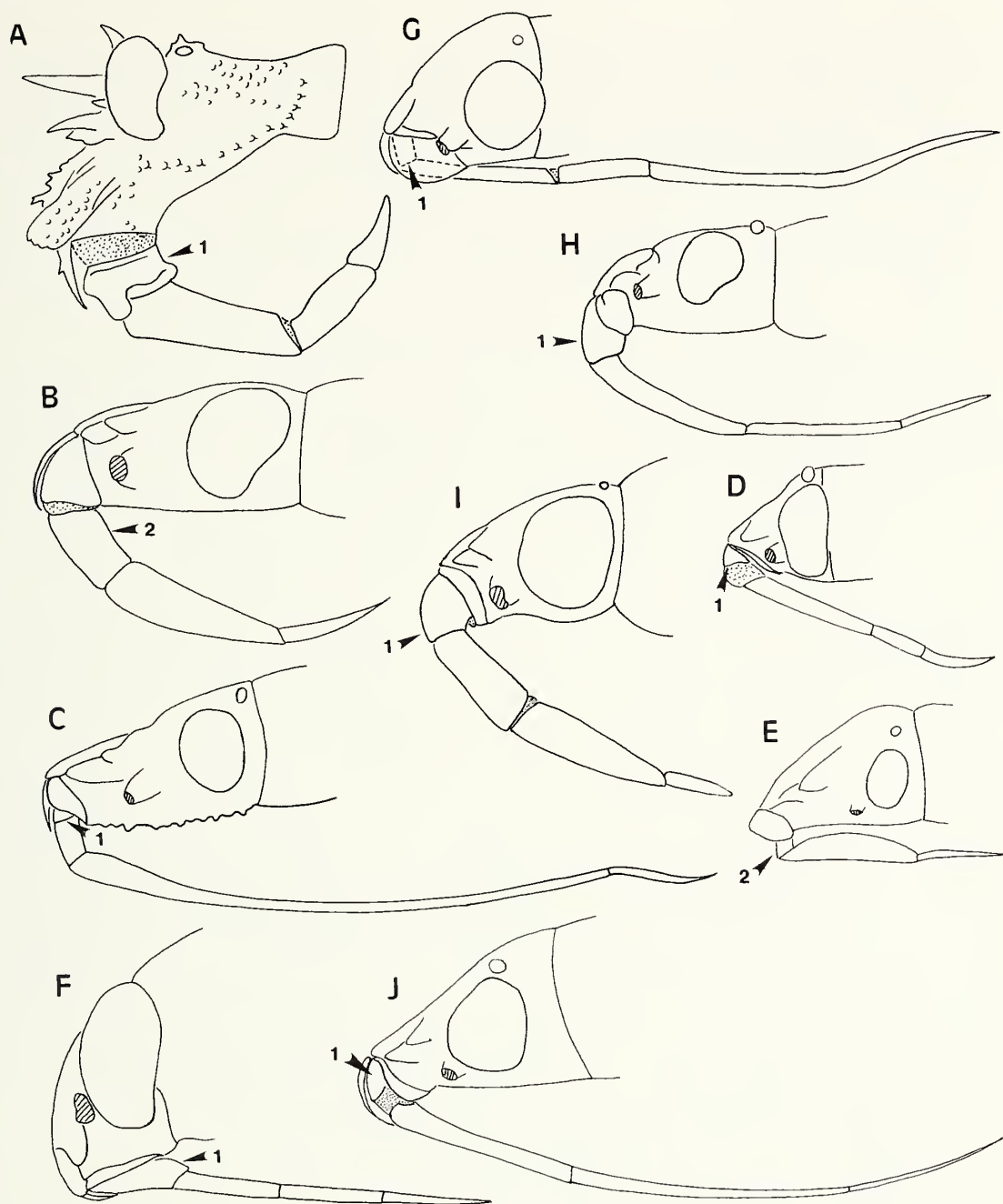
Fig. 5. Lateral view of heads of selected taxa of Cimicomorpha, illustrating conditions described for characters 9 and 10. **A,** Reduviidae, Centrocneminae (*Neocentrocnemis signoreti*; redrawn from Miller [1956a]); **B,** Pachynomidae (*Camarochilus* sp.); **C,** Velocipedidae (*Scotomedes alienus*; redrawn from Kerzhner [1981]); **D,** Microphysidae (*Chinaola quericola*); **E,** Joppeicidae (*Joppeicus paradoxus*); **F,** Miridae, Pilophorini (*Druthmarus philippinensis*; redrawn from Schuh [1984]); **G,** Medocostidae (*Medocostes lestoni*; redrawn from Štys [1967a]); **H,** Nabidae, Nabinae (*Nabis ferus*; redrawn from Kerzhner, [1981]); **I,** Nabidae, Prostemmatinae (*Pagasa guttula*; redrawn from Kerzhner [1981]); **J,** Lyctocoridae (*Lyctocoris campestris*).

and all cimicoid families except the Polyctenidae, in which segment 1 is developed similarly to segments 2–4. The reader should refer to Figure 5 for illustrations of selected taxa.

9. Labium type 0 (straight, appressed to ventral body surface, with segments 3 and 4 relatively long) occurs in the strictly phytophagous family groups, the predominantly phytophagous Miridae (Fig. 5F), and the Vianaidinae and Medocostidae (Fig. 5G) of unknown feeding habits. However, the labium in *Baclozygum,* in contrast to other

Thaumastocorinae, is extremely short, hardly exceeding the base of the head. Labium type 2 (Pachynomidae, Reduviidae; Fig. 5A, B, respectively), in addition to shortness, stoutness, and strong curvature, is characterized by its inflexibility (Cobben, 1978); the articulation between segments 2 and 3 is secondarily flexible in the Reduviidae, Triatominae (Lent and Wygodzinsky, 1979). Under character state 1 we have lumped all of the other admittedly rather diverse types of flexible, curved, or at least angularly bent labia, the subdivision of which (regardless of whether based on relative lengths of segments 2–4, type of curvature, or combination of both features) would have yielded only autapomorphies or imprecisely defined states.

Rieger (1976) and Kerzhner (1981) commented on the great similarity of shape and length of the labial segments in some Dipsocoromorpha (*Ceratocombus*), most Gerromorpha, Ochteridae, Aphelocheiridae, Saldidae, and cimicomorphans in the families Velocipedidae and some Lasiochilidae (*Lasiocolpus*; classified in the Anthocoridae *s. l.* by Kerzhner, 1981). The labium in these groups is characterized by short segments 1 and 2, a strikingly elongate segment 3, and a short segment 4 (Fig. 5C, J). Furthermore, the labium is essentially straight with a striking angularity between segments 2 and 3. Kerzhner (1981) regarded this type of labium as plesiomorphic within the Heteroptera and associated its function with the behavior of a searching predator; he further commented that the above mentioned groups never have raptorial forelegs. Kerzhner (1981) in his dendrogram regarded the velocipedid type of labium as unique among the Cimicomorpha, but inexplicably did not regard it as part of the ground plan for the clade including the Lasiochilidae. We found that the Joppeicidae, some Lasiochilidae (*Lasiochilus*), and some Anthocoridae *s. s.*, have essentially the same type of labium, but with the differences in the relative lengths of segments 3 and 4 not so great as in the Velocipedidae. The same is true for Lyctocoridae and Cimicidae, except that in them labial segment 2 is rather long. Segments 2, 3, and 4 are often subequal in length in the Microphysidae, Nabinae, Prostemmatinae (Fig. 5D, H, I); in the Microphysidae segment 2 is usually longest and segment 4 shortest (Fig. 5D; segment 4 is longest in *Ciorulla* [Péricart, 1974]). The Plokiophilidae are characterized by segment 4 being longer than the others (Carayon, 1974: figs. 11, 12), an attribute shared only with the Medocostidae. The Polyctenidae (coded 1 as well) are unusual in having an almost flaplike labium with all segments subequal in length (Ferris and Usinger, 1939: fig. 4).

10. The labial insertion in the Cimicomorpha can be divided into two more or less distinct types. In those groups in which most members are phytophagous the labium is inserted on the ventral surface of the head and at least the apex of the anteclypeus (tylus) is more or less vertical (Fig. 5F), except in most Thaumastocoridae (e.g., Slater and Schuh, 1990: fig. 1). The predatory groups have the labium inserted anteriorly on the head in a prognathous fashion, with the topographically upper surface of segments 1 or 2 often directed anteriorly and exceeding the apex of the anteclypeus; the anteclypeus is nearly horizontal (Fig. 5A–E, G–J). The only exception is the Polyctenidae with the base of the labium shifted far onto the ventral surface of the head (Ferris and Usinger, 1939: figs. 1, 4).

Thorax

11. The prosternal stridulatory sulcus is absent in several genera of Reduviidae (Miller, 1956b), but nonetheless appears to be part of the ground plan of the group.

Although we have coded the Thaumastocoridae as having the prosternal stridulatory groove, it is not present in all taxa and there is no evidence that it is in fact stridulatory. In *Discocoris* the groove extends onto the mesosternum (labium correspondingly long or longer) (pers. obs.). A similar situation may obtain in *Wechina* (Thaumastocorinae) were the labium exceeds the prosternum. The prosternum is provided with a medial longitudinal ridge in *Baclozygum* (Thaumastocorinae) with the labium being extremely short and not extending onto the prosternum (Drake and Slater, 1957).

12. In the Polyctenidae, nearly the entire metathoracic pleuron is modified into an evaporatory area but there is no distinct groove. A linear transverse slit parallels the anterior margin of the metapleuron but with no apparent connection to any internal structure (pers. obs.). Carayon (1971) confirmed the absence of the metathoracic scent gland groove in the Plokiophilidae, Microphysidae, and its strong reduction in the Pachynomidae and Reduviidae. Carayon and Villiers (1968) noted that in the Reduviidae a conspicuous groove on the metathoracic pleuron is actually associated with Brindley's gland rather than the true metathoracic scent gland.

13. The occurrence of paired metathoracic scent gland reservoirs (always combined with the presence of 2 widely separated ostioles [Carayon, 1971]) in Cimicomorpha is known in the Tingidae *s. s.,* Vianaidinae, Joppeicidae, Pachynomidae, and Reduviidae (Drake and Davis, 1960; Davis and Usinger, 1970; Carayon, 1971) and also in some Miridae, according to Staddon (1979). This type also occurs uniquely in the genus *Leptocimex* (Cacodminae) among the Cimicidae (Carayon, 1966). Davis and Usinger (1970) thought that the paired reservoirs of the metathoracic scent glands in the Joppeicidae possibly do not form a part of the usual metathoracic scent gland system, but belong to the so-called "ventral glands" which open at the thoracicoabdominal junction and are known to occur among the Cimicomorpha in the Reduviidae only; however, Carayon (1971) refuted this conjecture. We had to code the ground plan condition in the Leptopodomorpha as unknown since the situation in this infraorder (Cobben, 1970) is diverse, e.g., number of reservoirs/number of ostioles: Saldidae 1/1; Aepophilidae 2/2; Omaniidae 4/1; Leptopodidae: Leptopodini 2/2, Leotichiini 1/2 (unknown in Leptosaldinae).

14. Information concerning the presence of Brindley's gland is taken from Carayon (1950a), Drake and Davis (1960), and Carayon and Villiers (1968).

Abdominal Trichbothria

15. Ventral abdominal trichobothria in the Pachynomidae were first noticed by Štys in 1964, and subsequently mentioned in passing in the literature, with the first detailed documentation by Carayon and Villiers (1968). Ventral abdominal trichobothria in the Velocipedidae were discovered by Sweet (ms.) and their occurrence confirmed by us. Their position resembles that shown by Carayon and Villiers (1968: fig. 7) for the Pachynomidae, only they are situated closer to the abdominal midline, stiffer and much shorter. Carayon (1972b) suggested that some long, marginal to submarginal setae on the distal abdominal segments in the Anthocoridae *s. l.* and some other families, are of a trichobothrial nature; however, their true nature is yet to be demonstrated and they are surely not homologous with the medioventral trichobothria.

Legs

16. In nearly all groups for which the fossula spongiosa (for illustrations, see e.g., Lent and Wygodzinsky, 1979: fig. 17b, c; Carayon, 1972a: fig. 35) is indicated as present, there may be considerable variation on which legs it occurs, and not all species of a given group may possess the structure, or its occurrence may be limited to males. This structure is present in all families placed conventionally in the Cimicoidea, Nabidae *s. l.*, and Reduvioidea, including the Plokiophilidae and Polyctenidae (confirmed by our observation of specimens of *Lipokophila* sp. and *Eoctenes spasmae*, respectively). Detailed distribution for the fossula spongiosa in Kerzhner's (1981) broadly conceived Nabidae is as follows: Velocipedidae—absent; Medocostidae— vestigial on foretibia in males (not noticed in females by Štys (1967a); Nabinae— Nabini: fore- and middle tibiae in most genera (rudimentary in *Vernonia* and *Kerzhneria*), absent in *Metatropiphorus*; Carthasini: fore-, middle, and hind tibiae in *Carthasis,* fore- and middle tibiae in *Praecarthasis*; Gorpini: rudimentary on foretibia; Arachnocorini: absent in *Arachnocoris* (rudimentary on foretibiae in *Pararachnocoris*? [Kerzhner, pers. comm.]); Prostemmatinae—fore- and middle tibiae.

The tibial appendix in the Thaumastocorinae appears to be of a fundamentally different structure from the fossula spongiosa in other Cimicomorpha. It arises from a different part of the apex of the tibia as illustrated by Drake and Slater (1957: fig. 8). As emphasized by Kerzhner (1981) and confirmed by us, it is covered by unmodified hairs over its entire surface, rather than by modified microtrichia on the ventral surface only.

17. We have coded the number of tarsal segments according to what appears to be the ground plan condition for a given family. Within the Miridae, 2-segmented tarsi occur in all Isometopinae, Psallopinae, and some Cylapinae and Bryocorinae; because the Isometopinae appear to be the sister group of all other Miridae, we have treated the ground plan condition as 2-segmented. In the Plokiophilidae *Lipokophila* has 3-segmented tarsi (as found in most Cimicoidea), whereas in all other described genera the tarsi are 2 segmented. In the Nabinae Carthasini the *Carthasis* tarsal formula is 1-1-1, *Praecarthasis* 2-2-3 (Kerzhner, 1981, 1986). The tarsal formula is usually 3-3-3 in the Reduviidae, but in the Phymatinae, Phimophorinae, and Stenopodainae *partim,* it is 2-3-3 or 2-2-2, in the Reduviinae, 1-3-3, 2-3-3, or 3-3-3 (Putchkov, 1987), and in the Apiomerinae, Diaspidinae, and Ectinoderinae, the foretarsus may be 1- or 2-segmented or absent.

Ferris and Usinger (1939) correctly observed that the adult tarsal formula in the Polyctenidae is 3-4-4 and we have observed that in larval forms the tarsal formula is 2-3-3. Both of these conditions are unique within the Heteroptera. The additional segments are always the result of the separation of the basal portion of the distitarsus, understood here as a tarsomere without intrinsic musculature, articulating with the basal tarsal segment (basitarsus), and bearing the pretarsus. The novel segment in both larval and adult Polyctenidae is recognizable not only by its proximal position but also by the absence of pilosity. In other adult terrestrial Heteroptera the distitarsus is 1- or 2-segmented while in adult Polyctenidae it is 3-segmented on the middle and hind legs. The situation in adult Heteroptera when all tarsi are 1 segmented (some Enicocephalidae, Nepomorpha, and Nabidae) or the foretarsi only are 1 segmented (most Enicocephalomorpha, some Reduviidae and Nepomorpha), has not

been sufficiently well analyzed. These conditions may result from the complete suppression of the basitarsus or from its fusion with a nonsubdivided distitarsus.

18. Of the modern morphologists who discussed rotatory and cardinate metacoxae (occurring in so-called trochalopodous and pagiopodous Heteroptera, respectively), both Drake and Davis (1960) and Cobben (1978) agreed that this historical distinction is somewhat artificial and that intermediate types exist. Cobben (1978) emphasized that the really important distinction is the presence or absence of a trochantin. Nevertheless, the external shape and mobility of the metacoxa in the Cimicomorpha are so diverse that we attempted to include the forms originally recognized by Schiødte (1870), but also included intermediate types. In the case of the Nabinae, which possess cardinate and intermediate types, and the Reduviidae which possess rotatory and intermediate types, we coded each group for the modal condition. Even with this attempt at more precise characterization, the coxae appear to contain little or no information of phylogenetic value and we therefore did not include them in our final analysis.

Wings

19. We have treated the costal fracture as part of the ground plan for the Heteroptera, owing to its occurrence in some members of all infraorders, except the Gerromorpha and Pentatomomorpha. The Saldidae and some other leptopodomorphans possess a well developed costal fracture which arcuately joins the medial furrow (e.g., Polhemus, 1985: fig. 29e, f, h), delimiting an elongate triangular cuneus; we have therefore coded the Leptopodomorpha as having a cuneus, although it is never referred to as such in the literature.

Within the Cimicomorpha, the suggestion that the presence of a long costal fracture (=cuneal incisure, cuneal fracture) demarcating a cuneus can be used to form a group uniting the Microphysidae, Miridae, and Cimicoidea *s. s.* appears to be contradicted by our analysis, by virtue of overlooking the presence of this structure in other cimicomorphans (Velocipedidae, Prostemmatinae, Pachynomidae). The occurrence of the costal fracture in the Pachynomidae (present in *Pachynomus, Punctius*) and Prostemmatinae (present but usually very short in some *Pagasa* and *Prostemma*) is not constant. Because some members of both groups possess the costal fracture, we have coded them as if all members possessed it. The costal fracture in *Punctius* and the Prostemmatinae just interrupts the costal margin, or is rarely longer (Kerzhner, 1981; pers. obs.); it is rather short in *Pachynomus* as well, and there is no distinct cuneus (Carayon and Villiers, 1968; pers. obs.).

20. Most known specimens of Vianaidinae are strongly coleopteroid, and therefore the attributes of venation in the forewing are almost totally obscured. As mentioned above, macropterous specimens have a carinate medial vein running the entire length of the corium similar to the situation found in *Joppeicus paradoxus*. This condition also appears to exist in most, if not all Tingidae *s. s.,* even though the forewings are highly modified and the condition in the Cantacaderinae is somewhat complex. Because of this observation, and the apparent close relationship of the Tingidae *s. s.* and Vianaidinae on the basis of other attributes, we have coded the former group as possessing the carinate medial vein.

21–22. Venation of the forewing membrane has traditionally been used to diagnose higher taxa and establish phylogenetic relationships in the Cimicomorpha. However,

recognition of clearly defined character states has proved difficult. Therefore, we offer some explanatory remarks and survey briefly the situation in individual families.

Carayon (1977b) recognized two basic types of veins in the membrane: live veins which retain living cells throughout the adult life of the insect, contain neurons and are provided with sensilla; and dead veins, which contain no living cells and are devoid of sensilla. Kerzhner (1981, including fig. 98) studied this character complex comparatively and employed it in his phylogenetic analysis of the Cimicomorpha, using as a criterion for live veins the presence of macrotrichia and/or campaniform sensilla. According to him the ancestral situation obtains in the Leptopodomorpha (e.g., Saldidae) with 4, elongate, simple cells formed by live veins. In three families of Cimicomorpha cells formed by live veins are preserved: Velocipedidae with 3 or 4 short live cells (cell 1, beginning at the costal margin, open, if present; closed cells 2, 3, and 4 always present); Miridae usually with 2 short live cells (cell 1, and fused 2–4); and Microphysidae with 1 short live cell (fused cells 2–4). Kerzhner assumed that all other membrane venation in the aforementioned families is dead, and that in the Medocostidae, Nabinae, Prostemmatinae, and cimicoid families the original live cells have been compressed into a vein forming the boundary between the corium and membrane and diverging slightly onto the membrane distad of the cuneus and terminating there as a "stub" (*processus corial*; Carayon, 1974, 1977b), homologous to a similar structure found in the distal corner of cell 2 in the Velocipedidae and of fused cells 2–4 in the Microphysidae. The Pachynomidae, Reduviidae, and Joppeicidae, Tingidae, and Thaumastocoridae should have no live venation on the membrane or at the corium-membrane boundary under Kerzhner's theory.

As mentioned elsewhere in this paper, when we tried to code Kerzhner's theory of membrane venation into clear-cut character states, we found little congruence with other characters. We concluded that a more traditional interpretation of membrane venation showed greater consistency with other characters. Under our hypothesis the membrane cells in the Medocostidae, Nabinae, Prostemmatinae, Pachynomidae, and Reduviidae could be viewed equally well as derived from the original elongate cells. The venation of many Phymatinae, with short basal cells and many emanating veins, is strongly reminiscent of the condition found in the Velocipedidae. The simple membrane venation occurring in some reduviid taxa is best explained by the subsequent opening of the cells as, e.g., in the Elasmodeminae (Putchkov, 1987; pers. obs.).

We found the "stub" (processus corial), first employed as a systematic character by Kerzhner (1981), to be particularly useful. This rounded to truncate projection (or termination) of a vein is situated distad of the cuneus and never reaches the costal margin of the membrane. In many Lasiochilidae and Anthocoridae the membrane venation is reduced, and the stub or its remnant appears as a semisclerotized bulgelike structure isolated on the membrane (Fig. 7F). Although the stub is barely visible on the upper wing surface in the Prostemmatinae, it is sharply delimited on the lower forewing surface, appearing as an elongate, slightly raised, platelike structure.

The venational details of individual families can be characterized as follows:

Velocipedidae: Cells 2, 3, and 4 present but abbreviated and situated at base of membrane. Cell 1 open (absent) or closed by a feeble rudimentary vein; numerous veins radiating posteriorly from the cells; stub present on apex of cell 2, easily visible on lower wing surface (Fig. 6D; Kerzhner, 1981: fig. 24).
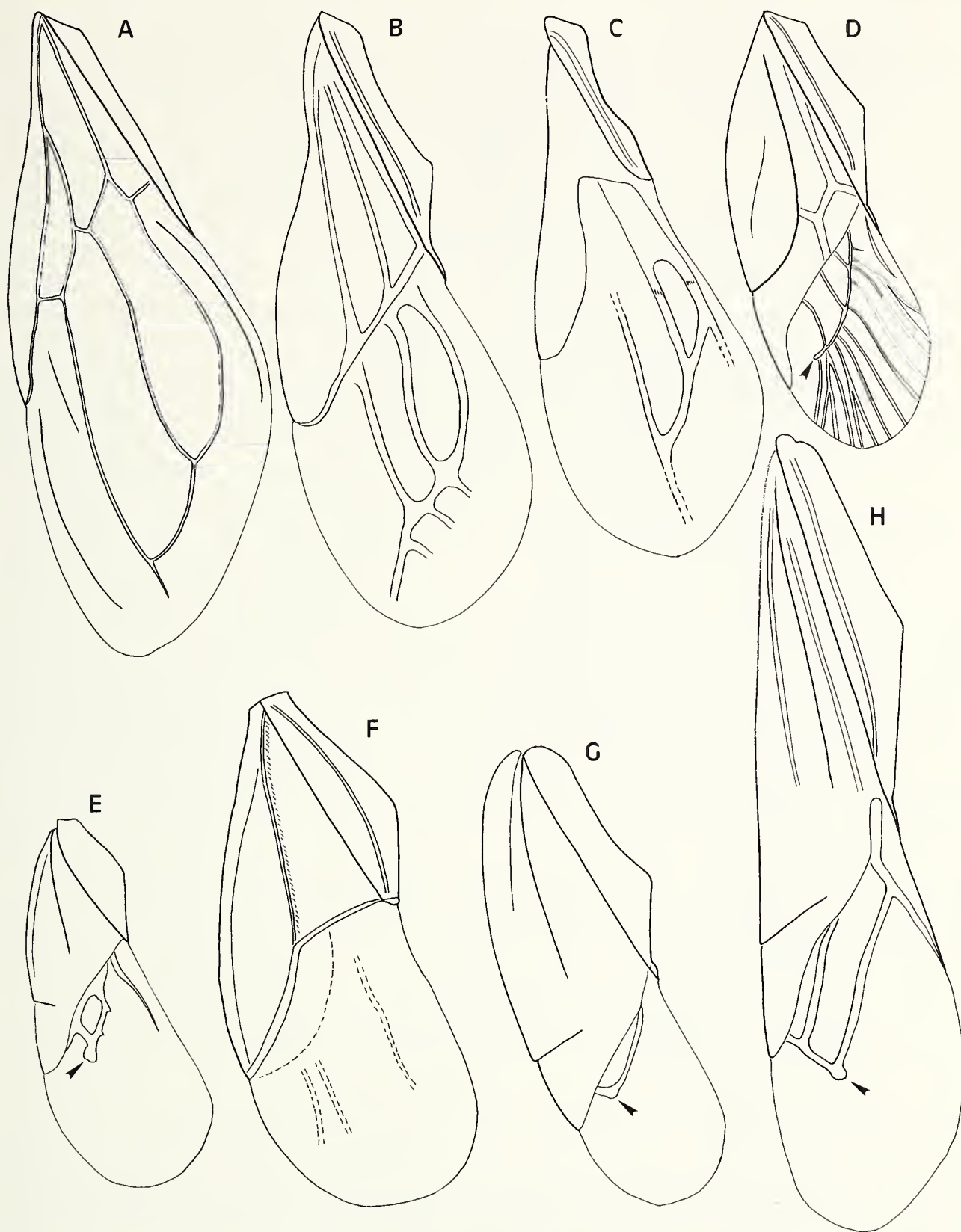
Fig. 6. Forewings of Cimicomorpha, demonstrating essential attributes of corium and clavus and details of membrane described for characters 21 and 22. **A,** Reduviidae, Triatominae (*Triatoma guazu*; redrawn from Lent and Wygodzinsky [1979]; **B,** Pachynomidae, Pachynominae (*Camarochilus* sp.); **C,** Pachynomidae, Aphelonotinae (*Aphelonotus* sp.); **D,** Velocipedidae (*Scotomedes* sp.); **E,** Microphysidae (*Myrmedobia exilis*); **F,** Joppeicidae (*Joppeicus paradoxus*; modified from Davis and Usinger [1970]; **G,** Miridae, Isometopinae (*Corticoris signatus*); **H,** Miridae, Cylapinae (*Cylapus* sp.). Position of stub indicated by arrow.
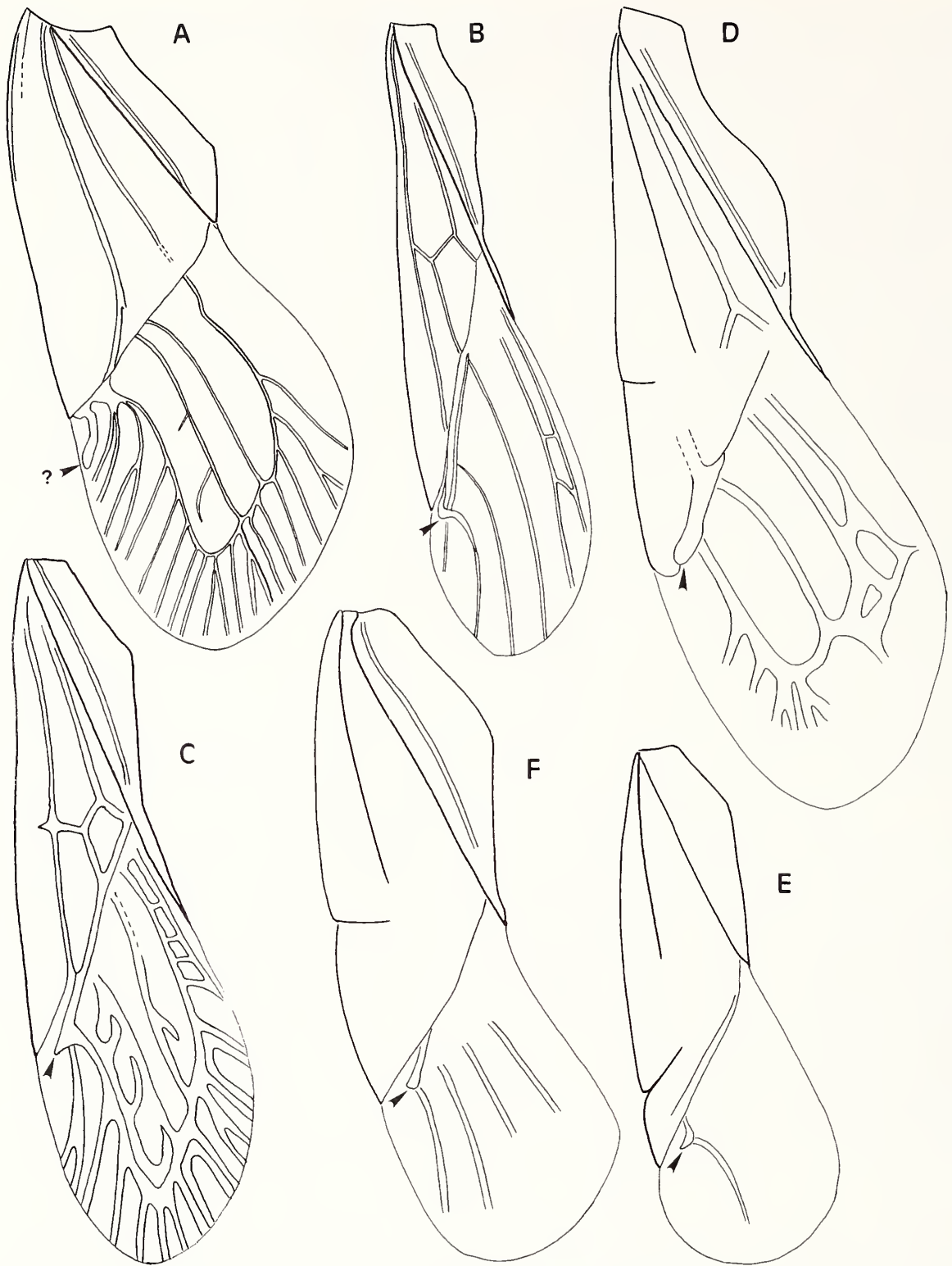
Fig. 7.   Forewings of Cimicomorpha, demonstrating essential attributes of corium and clavus and details of membrane described for characters 21 and 22. **A,** Medocostidae (*Medocostes lestoni*; redrawn from Štys [1967a]; **B,** Nabidae, Nabinae (*Metapterus alvarengai*); **C,** Nabidae, Nabinae (*Nabis americoferus*); **D,** Nabidae, Prostemmatinae (*Pagasa luteiceps*); **E,** Plokiophilidae (*Lipokophila* sp.); **F,** Lyctocoridae (*Lyctocoris campestris*). Position of stub indicated by arrow.

Miridae: Two abbreviated cells (Fig. 6H) (under Kerzhner's interpretation, 1 adjacent to cuneus, fused 2+3+4 medial) sometimes merging into a single cell, e.g., some Isometopinae (Fig. 6G) and Bryocorinae. Usually no longitudinal veins except a single one near the morphologically posterior margin of the membrane, rarely a

few simple veins emanating from the posterior margin of the large cell in some large Mirini and a few Odoniellini (Bryocorinae) (Carayon, 1977b; fig. 1); stub present at distal angle of cell(s). Carayon (1974, 1977a) considered the membrane veins in part to represent the stub (processus corial) and indeed our observations (Fig. 6G, H) indicate that his observation may be correct.

Microphysidae: One short, more or less quadrate, cell (fused cells 2–4 ?) formed of strongly sclerotized veins, situated medially at the base of the membrane, remote from cuneus, with 4 or 5 longitudinal veins emanating posteriorly and 1 free simple posterior vein; stub present at apex of cell (Fig. 6E; Péricart, 1972: fig. 9a).

Medocostidae, Nabinae, Prostemmatinae: Two or 3 long cells (not associated with apicocorial area), with many emanating veins (Fig. 7A–D); cells open and venation simplified in various Nabinae and Prostemmatinae (Phorticini; Štys, pers. obs.); stub present (absent in at least some Phorticini), often elongate, associated with corium–membrane boundary (Nabidae—Kerzhner, 1981: fig. 26) or slightly removed (Medocostidae—Štys, 1967a: fig. 21; Fig. 7A).

Pachynomidae: Two, long, "reduvioid" cells with many emanating veins (*Pachynomus*) or emanating veins faint and few (*Camarochilus*) or reduced to 1 (*Punctius, Aphelonotus*); no stub (Fig. 6B, C).

Reduviidae: Two or 3 long closed cells with or without 1 emanating vein and with or without 1 free posterior vein (Fig. 6A), rarely with 4 free veins (Elasmodeminae) or with 2 short basal cells (sometimes more numerous and variable in number) with many emanating veins and 2 posterior free branching veins (Phymatinae); no stub (Fig. 6A). Although Kerzhner (1981) treated all reduviid venation as dead, Davis (1961) clearly showed tracheation of membrane cells in the group.

Lasiochilidae, Lyctocoridae, Anthocoridae: Four or 5 simple free veins; stub present, associated with corium (cuneus)-membrane boundary, sometimes detached (Fig. 7F).

Plokiophilidae: Membrane sometimes apparently with 1 or 2 elongate cells (Carayon, 1974: figs. 5, 7), or closed cells absent and a single vein projecting distally from stub (Fig. 7E); stub present, projecting from corium-membrane boundary (Carayon, 1974: fig. 31; Fig. 7E).

Joppeicidae: Large transverse cell formed by a fold (foldlike vein ?), with 2 emanating simple veins and 1 free posterior vein; no stub (Fig. 6F); Drake and Davis, 1970: fig. 6).

Tingidae *s. s.*: Major longitudinal veins continuing onto membrane area (not differentiated from corium); no special membrane venation; no stub (Drake and Davis, 1960: fig. 13).

Vianaidinae: No membrane venation, no stub, including macropterous forms (pers. obs.).

Thaumastocoridae: No membrane venation; no stub (Drake and Slater, 1957; pers. obs.).

23. The distal free sector of R+M (emanating from the hind wing cell) is usually simple in the Cimicomorpha. However, Davis (1961) and Štys (1962) found that it branches into free distal sectors of R and M in the Nabinae and Microphysidae. Štys (1967a: fig. 25) found that R+M has several short lateral branches in the Medocostidae, but the morphological identity of the distal branching veins seems in doubt. Carayon (1970), on the basis of studying the tracheation of the Nabinae suggested

that the posterior sector of the branching R + M is actually only a secondary branch of the media, its major part remaining captured by R. On the other hand, Leston (1962) concluded that the distal sector of veins R, M, and Cu is not tracheated at all. The illustration of the hind wing of *Pachynomus picipes* by Carayon and Villiers (1968) suggests inconclusively that branching R + M may also occur in some Pachynomidae, but because it does not occur in other genera, we coded it as absent in the family.

24. The media (as interpreted by Davis, 1961) in the hind wing runs within the closed cell and meets as a long vein or a stumplike hamus either Cu or the point where the free distal sector of Cu diverges from the cell (in these two cases the "cross vein" closing the cell and meeting R is actually formed by M), or joins the above "cross vein" (e.g., Davis, 1961: fig. 16); in the latter case the "cross vein" is formed in part by a true cross vein m-cu and in part M. The presence of a true m-cu cross vein is characteristic of most families of Cimicomorpha as shown in the matrix. However, its presence in Plokiophilidae (documented in *Lipokophila* sp. only), Anthocoridae (Carayon, 1972a), Pachynomidae (Carayon and Villiers, 1968), and Reduviidae is a ground plan character only and the situation in all of these families is diverse. Davis (1961: fig. 29) illustrated the hind wing of *Scotomedes ater* (Velocipedidae) as lacking m-cu, but it is definitely present in a species of Velocipedidae from New Guinea. In several families of Cimicomorpha the true m-cu cross vein seems to be consistently absent: Microphysidae, Miridae, Joppeicidae, Thaumastocoridae, and Tingidae. We include here also the groups where any remnant of M within the cell is missing and M is represented only by a transverse vein closing the cell. Data for the matrix were extracted from Davis (1961), Štys (1967a), Carayon and Villiers (1968), Kerzhner (1981), and Carayon (1972a); the condition in the Velocipedidae and Plokiophilidae was reexamined.

Abdomen

25. The presence of dorsal laterotergites is undoubtedly part of the ground plan of the Cimicomorpha. However, in some taxa these structures are found associated with only certain abdominal segments, e.g., in the Lasiochilidae as distinct entities on abdominal segments 1 and 2 only (Carayon, 1972a). In such cases we have coded dorsal laterotergites as present for the taxon. The unusual structure of the abdomen in the Joppeicidae (Davis and Usinger, 1970: figs. 8, 12) has caused confusion concerning whether the distinct laterotergites are dorsal or ventral in origin; we have followed Sweet (1981) in interpreting them as dorsal. The abdominal dorsum in the Microphysidae is desclerotized in the males and sclerotized in the females, but distinct laterotergites are not present. The presence of dorsal laterotergites in the Plokiophilidae is based on observation of *Lipokophila* sp. According to Carayon (1972a) all of the Lasiochilidae, Lyctocoridae, and Anthocoridae have dorsal laterotergites at least on some segments, with the exception of *Astemmocoris,* a genus of questionable placement.

26. As with the dorsal laterotergites, if the ventral laterotergites are present at least in some taxa, or some segments only, or in males only, they were coded as present. The ventral laterotergites in the Velocipedidae are present only in the males (Sweet, ms; pers. obs.), but are not evident in the females and apparently fused with the sternum. We consider the ventral spiracle bearing plate in the Joppeicidae to represent

the fusion of the sternum and the ventral laterotergites (Sweet, 1981). Although the ventral laterotergites are coded as being absent in the Prostemmatinae, the original boundary of the structure is demarcated by a ridge on the venter in the Phorticini. We have coded these structures as present in the Nabinae, although they are absent in some genera. The Polyctenidae are unusual among the Cimicoidea in the possession of ventral laterotergites.

27. The presence or absence of the first abdominal spiracles, as coded in the data matrix, seems unproblematic, except for the taxa discussed below. The occurrence of the first abdominal spiracle in the Thaumastocorinae was noted by Drake and Slater (1957). Its occurrence was confirmed by us in the sclerotized lateral part of the first tergum of *Discocoris* (Xylastodorinae); it was observed in the membrane between the metanotum and the first abdominal tergum of *Thaumastocoris australicus, T. hackeri* (Thaumastocorinae) and *Xylastodoris luteolus* (Xylastodorinae) by Sweet (ms). It is not apparent that any of these observations include the documentation of tracheal connections. The absence of the first abdominal spiracle in the Joppeicidae, as indicated in the matrix, was noted by Davis and Usinger (1970). The absence of the first abdominal spiracle in the Microphysidae and Velocipedidae was confirmed by our own examination of *Myrmedobia exilis* (see also Štys, 1962) and *Scotomedes* sp., respectively.

28. Our observations on spiracle positions on the abdomen confirm those of Sweet (ms). We have coded the Joppeicidae as in other Miriformes and Cimiciformes where the spiracles are situated on a sclerite formed by the fusion of the sternum and the ventral laterotergite. Alternatively, in the Reduvioidea, the spiracles are situated on the true sternum, mesad of the line delimiting the ventral laterotergites.

29. Fossettes parastigmatiques (parastigmal pits) were first discovered by Carayon (1948: figs. 1, 2; 1950b: figs. 1, 2). These small structures are situated on the ventral laterotergites and contain a cluster of secretory hairs; their function is unknown. They occur in Nabinae (Nabini and some Carthasini [*Praecarthasis* Kerzhner, 1981, 1986], on segments 3–7 with the most restricted occurrence on segment 7 only, but are absent in *Carthasis*, Arachnocorini, and Gorpini) (Kerzhner, 1981; Carayon and Villiers, 1968). In the Prostemmatinae, Prostemmatini they occur as a single pair on segment 3 and are absent in the Phorticini (Kerzhner, 1981). Similar appearing structures are found on the second abdominal segment in the Pachynomidae, Aphelonotinae, and as less well formed structures in the Pachynominae, whereas they are completely absent in *Punctius* (Carayon and Villiers, 1968). Kerzhner (1981) presumed that the fossettes parastigmatiques in Nabidae and Pachynomidae are homologous and that they are secondarily absent in the Reduviidae; both conclusions appear to be incorrect in light of our analysis.

30. The apophysis is a small anteriorly directed, median, internal projection of the anterior margin of abdominal sternum 7 in the female. Its distribution is based on the works of Štys (1967a: fig. 43), Carayon and Villiers (1968), Carayon (1972a), Ford (ms), and Kerzhner (1981). It is apparently secondarily absent is the Arachnocorini (Nabinae).

31–34. Cobben (1978:141, table 2) summarized the distribution of the dorsal abdominal scent glands in larval Heteroptera. We checked the distribution in all families where Cobben's summary was ambiguous or lacked information entirely (Thaumastocoridae, Velocipedidae [first observation of actual larval gland openings],

Microphysidae, and Polyctenidae). In the Lasiochilidae (our observations), Medo-costidae (Štys, 1967a), and Pachynomidae (Cobben, 1978), the recorded occurrence is based on the presence of scars in the adult abdomen because larvae are unknown or unstudied. The orifices of glands 3/4, 4/5, and 5/6 in larvae are always associated with the actual glands. Orifices between segments 6 and 7 have functional inner glandular parts only in the Joppeicidae; external nonfunctional scars of orifices on 6/7 remain in several additional families. The determination of whether scars actually exist is sometimes a subjective judgment, and therefore no great value can be placed on this character. Scars and glands are usually located on the anterior margin of the more posterior segment. Most observers have not found larval abdominal scent glands in the larvae of the Polyctenidae. Ferris and Usinger (1945) noted that dorsal scent glands were present on the posterior margins of abdominal segments 4, 5, and 6 (clearly a *lapsus calami* for "anterior margins") in some larval Brazilian specimens, and that the glands resembled those of the Cimicidae.

35. Ekblom's organ, a structure first noticed by Ekblom (1926: figs. 56, 57) and later named for its founder by Kerzhner (1981: fig. 60b), occurs in males of all Prostemmatinae and most Nabinae (Kerzhner, 1981). It consists of two diagonal grooves surrounded by specialized setae situated behind the posterior foramen of the pygophore (Carayon, 1970: fig. 20) and a group of specialized setae at the postero-apical margin of the hind femur. Males possessing the organ rub the tibiae across the pygophoral portion of the organ and distribute attractant pheromones from intrarectal glands (Carayon, 1970); previously the organ was thought to be part of a stridulatory apparatus (Ekblom, 1926), but Leston (1957) considered such a function unlikely.

36. The data from Kerzhner (1981) regarding reduction of abdominal segment 8 in males are accepted here and have been reconfirmed by us for several families. We have coded this character as occurring in the primitive condition in the Nabinae, because it is found in that condition in *Metatropiphorus,* the genus which Kerzhner believed to be the most primitive within the Nabinae (Nabini).

Genitalia and Insemination

37. Male terminalia (essentially the pygophore and parameres) are asymmetrical in several families; we recognize three types, each of them appearing to have evolved independently. In the thaumastocorid type, (state 2), described by Drake and Slater (1957: figs. 6, 8, 11), the pygophore is strongly asymmetrical and turned laterad, the asymmetry strongly affecting one or more abdominal segments anterior to 9, one or both parameres are lost, and the asymmetry is either sinistral or dextral. In the mirid type (state 1) the parameres and pygophore are asymmetrical, the asymmetry is always sinistral but not affecting the abdominal segments anterior to the pygophore, both parameres are retained and never lanceolate or horizontal. In the cimicoid type (state 3), except in the Plokiophilidae, the sinistral asymmetry affects the parameres and pygophore, but abdominal segment 8 is at most slightly asymmetrical, the left par-amere is dominant, more or less lanceolate, and its blade is oriented horizontally and directed more or less perpendicular to the longitudinal axis of the pygophore.

In some families where parameres are usually symmetrical, there are isolated cases of asymmetry, e.g., in most Peiratinae (Reduviidae) and some Nabinae and Pros-

temmatinae (Kerzhner, 1981). In all of these cases we consider the ground plan condition to be symmetrical. In some groups one of the parameres, usually the right, has been lost completely. These include all of the Cimicidae and Polyctenidae (see e.g., Ferris and Usinger, 1939; Usinger, 1966), and some Lasiochilidae and Anthocoridae (Carayon, 1972a). In the Thaumastocorinae, only one paramere is present, being either the right or the left (genus specific or species specific attribute), while in the Xylastodorinae the same species may be dextrally or sinistrally asymmetrical, with *Discocoris* retaining a single paramere, and *Xylastodoris* uniquely having lost both parameres (see Drake and Slater, 1957). We have regarded the parameres in the Plokiophilidae as symmetrical, and indeed this seems to be the case for most genera. Nonetheless, Štys (1967b) and Eberhard et al. (in prep.) have shown that in the genus *Lipokophila* the parameres are of a slightly different size and shape even though the pygophore appears to be symmetrical; however, Carayon's (1974) illustrations of *Lipokophila* would suggest that the parameres are symmetrical.

38. Carayon (1972a, etc.) and Ford (ms.) have discussed the structure and summarized the distribution of the copulatory paramere in the Cimicoidea. See also notes under character 40 for functional explanation.

39. The orientation of the parameres was used by Kerzhner (1981) as a character and we have employed his data. In the Pachynomidae the basal portion of the parameres points caudad with the distal portion directed cephalomesad. There are other aspects of paramere direction and insertion which could be employed in phylogenetic analysis, but a comparative survey is not available. For example, within the families studied in detail by Kerzhner (1981), the situation is as follows: parameres situated on dorsum or sides of pygophore (and directed cephalad—Velocipedidae and most Nabinae; or cephalomesad—Nabini, *Metatropiphorus*; or dorsomesad—Medocostidae); situated caudad and directed dorsad—Prostemmatinae, Prostemmatini; situated ventrad, owing to ventral position of pygophore, and directed caudad (but morphologically cephalad)—Prostemmatinae, Phorticini.

40. The term acus used by Carayon (e.g., 1972a) refers to the so-called "needle of injection." This is the apical spinelike process of the phallus as found in many Cimicoidea and apparently all Prostemmatinae (e.g., Carayon, 1970a: fig. 26).

For the reader not familiar with the specialized morphology and type of copulation found in the Cimicoidea we offer a brief explanation of the functional relationship between the phallus and left paramere. In the Lasiochilidae, Plokiophilidae, and Lyctocoridae, the phallus itself serves as the intromittent organ; in Lasiochilidae there is no acus and no traumatic insemination, whereas in the Plokiophilidae and Lyctocoridae the acus penetrates the integument of the abdominal wall, and in a similar way penetrates the vaginal wall in the Prostemmatinae. There is a specialized relationship between the phallus and left paramere in the Cimicidae, Polyctenidae, and Anthocoridae, where the left paramere penetrates the abdominal wall or the metacoxal arthrodial membrane of the female and insemination is always traumatic. In these groups, excepting the Anthocorini *sensu* Carayon and Scolopini (*vide* Péricart, 1972), the distal portion of the phallus is reduced to a short membranous tube situated within the parameral groove and serves only for introduction of sperm into the abdominal cavity of the female. In the Anthocorini and Scolopini the phallus is long, not accommodated in the parameral groove and slides into the copulatory tubes of the female (see Carayon, 1966, 1970, 1971, 1977a). In these last two groups the

details of the functional relationship between the phallus and the left paramere needs to be investigated in greater detail (see conflicting reports by Carayon [1972a] and Péricart [1972]).

41. The reduction of the ovipositor in the Cimicomorpha, as for the Heteroptera in general, has occurred many times, as seems obvious from our analysis. In four groups we coded the ovipositor as laciniate, whereas some members of those groups actually have it plate-shaped or greatly reduced. These are: Nabinae, Arachnocorini, *Arachnocoris* (Kerzhner, 1981); Prostemmatinae, excluding Phorticini (Kerzhner, 1981); Lasiochilidae and Anthocoridae, diverse genera (Carayon, 1972a).

Information on the loss of a connection between the first valvula and the first valvifer in those groups with a laciniate ovipositor (character state 1) is taken from Drake and Davis (1960). However, the Microphysidae, coded as having the primitive condition, might not have been investigated for this attribute and should be reexamined.

42. The information on relationships between ventral laterotergite 8 and valvifer I provided in the matrix is based mostly on the information given by Scudder (1959) and Drake and Davis (1960) and supplemented by information on the Pachynomidae (Carayon and Villiers, 1968), Medocostidae (Štys, 1967a), Joppeicidae (Davis and Usinger, 1970), and Prostemmatinae (Kerzhner, 1981). The condition in *Lasiochilus* has not been studied, but the retention of the plesiomorphic condition (ventral laterotergite free) is probable. Kerzhner (1981) observed that valvifer I is fused with laterotergite 8 in some Nabinae (*Arachnocoris*) and Prostemmatinae (Phorticini). The same condition may apply to those Lasiochilidae and Anthocoridae with a reduced ovipositor. In the Tingidae ventral laterotergite 8 is fused with valvifer I, but it is still recognizable as a distinct entity; we coded it as fused.

43. In many cimicomorphans, the spermatheca is transformed into a so-called vermiform gland (in Reduviidae, e.g., Davis, 1966: fig. 39; in Miridae, e.g., as spermathecal gland, Davis, 1955: fig. 7) which has no sperm storage function. *Joppeicus* retains a structure with all the components of a true spermatheca, but it is small and not functioning as a sperm storage structure (Carayon, 1954: figs. 5–7; Carayon in litt. to Kerzhner, 1981; Davis and Usinger, 1970: fig. 17). In the Tingidae *s. s.* a "reduced spermatheca" is present in some Cantacaderinae only (Kerzhner, 1981 [according to Carayon, in litt.]; Péricart, 1983), whereas in other Cantacaderinae and Tinginae it is completely absent. However, Drake and Davis (1960: fig. 15) illustrated a "spermathecal gland" in *Cantacader quadricornis* and considered it to be a reduced vermiform gland. (For organs functionally replacing the spermatheca in the Tingidae see discussion of character 45 below.) We have treated the reduced nonfunctional spermatheca as part of the ground plan of the Tingidae. According to Scudder (1959) and Drake and Davis (1960) the spermatheca (or its homolog) is absent in the Vianaidinae. Kerzhner (1981) quoted Carayon (in litt.) as stating that *Embiophila* (Plokiophilidae) has a typical small spermatheca with a bulb and duct; he considered it as possibly a new structure similar to that occurring in *Plokiophiloides* (Carayon, 1974). We have tentatively accepted Carayon's (1974) opinion concerning the occurrence of a "vestigial spermatheca" in the Plokiophilidae.

44. Information summarized by Carayon (1977a) indicates that spermatolytic bodies are groups of amoebocytes and macrophages located at the bases of the ovarioles. Their function is the destruction and resorption of excess spermatozoa. They are

formed by individual cells in the Prostemmatinae, whereas they are of a syncitial nature in the Cimicoidea.

45. The Reduviidae and Pachynomidae possess paired, tubular pseudospermathecae opening into a median oviduct (Davis, 1966: fig. 36) and serving as permanent sperm storage organs in place of the typical heteropteran spermatheca. In the Pachynomidae these structures are visible only after clearing (Carayon and Villiers, 1968: figs. 26–28), being covered by the muscular tunica of the ovipositor. Analogous paired organs, serving for only temporary sperm storage, are the large, subglobular, paired ectodermal seminal sacs of the Tingidae s. s. (Carayon, 1954: figs. 1, 3; Drake and Davis, 1960: fig. 12), opening into a median oviduct (or even the gynatrium) or into the broad proximal ectodermal parts of the lateral oviducts. It is uncertain whether these paired seminal sacs are homologous to the functionally equivalent median unpaired ectodermal dorsal sac (often referred to as the seminal sac [e.g., Carayon, 1954]) of the Miridae and at least some Cantacaderinae (Drake and Davis, 1960: fig. 25). Paired, broadly tubular spermathecal organs associated with the lateral oviducts found by Drake and Davis (1960: fig. 25) in *Cantacader quinquecostatus* jointly with the dorsal sac are of mesodermal origin and are not homologous with psuedospermathecae. Drake and Davis (1960) concluded that a possible homology between pseudospermathecae, seminal sacs, and the dorsal sac is ambiguous, and we regard the true psuedospermathecae of reduviids and pachynomids as structurally and functionally unique.

46–47. The method of fertilization in the Cimicomorpha has been studied in great detail by Carayon with the results presented in numerous papers (1954, 1957, 1966, 1972a, 1977a, etc.). The situation in the Vianaidinae, Thaumastocoridae, Velocipedidae, and Medocostidae is inferred from examination of gross morphology rather than functional studies. Carayon (1962a) pointed out the three different modalities of fertilization which exist in the Cimicomorpha: 1) Reduvioidea—in ectodermal part of the female reproductive tract; 2) most other groups (Tingidae s. s., Vianaidinae, Miridae, Microphysidae, Joppeicidae [*contra* Carayon, 1962a], Lasiochilidae, Nabinae, and Prostemmatinae [the last even in spite of traumatic insemination])—in lateral mesodermal oviducts or in the ovarial pedicels; and 3) cimicoid families less Lasiochilidae—in the vitellarium. Carayon (1972a) stressed the similarity in fertilization between the Prostemmatinae and Lasiochilidae (cf. Carayon, 1957), but did not comment upon what he supposed to be the similarity between the situation in the Joppeicidae and the advanced cimicoid families. Davis and Usinger (1970) examined the mode of fertilization in the Joppeicidae and found that insemination actually takes place according to mode 2, not as in the cimicoid families. Hemocoelic (traumatic) insemination among the Heteroptera is restricted to the Cimicomorpha. In the Cimicoidea it is ordinarily accomplished by penetration of the left paramere and/ or phallus through nonspecialized to highly modified regions (i.e., ectospermalege, mesospermalege [also variously referred to as Berlese's organ or Ribaga's organ], copulatory tubes, etc.) of the abdominal wall of the genital or pregenital segments. Only in Polyctenidae are the sperm introduced into the hemocoel via the arthrodial membrane of the right metacoxa. In the Prostemmatinae the vaginal wall is punctured by the phallus. For a summary see Carayon (1977a). See also discussion of character 40. Cobben (1968) alluded to the possibility of accidental traumatic insemination in the Microphysidae and vitellarial insemination in the Velocipedidae (micropyle re-

duced and solid) and Nabinae, Arachnocorini (micropyle absent), but in our view these suggestions require confirmation through additional observation.

Eggs

48. Data for micropyle numbers are from Cobben (1968), who stated that there are no distinct external micropyles in either the Thaumastocorinae or Xylastodorinae and that the aeropylar system seems to be combined with the micropylar system in a different way in each of the two subfamilies. Some Nabinae (Arachnocorini) have lost the micropyles. Cobben (1968) was not sure whether 1 or 2 micropyles occur in the Microphysidae; we have coded 1. The Polyctenidae have pseudoplacental viviparity and do not form a chorion (Hagan, 1931). Davis and Usinger (1970) described the eggs of the Joppeicidae as having 1 micropyle.

Habits

49. For the Vianaidinae, Velocipedidae, and Medocostidae, where no observations on feeding habits are available, we have coded this character as unknown. For the Miridae, even though most species are phytophagous, we have coded the group as predaceous because the most primitive subgroup, the Isometopinae, is predaceous. Some Anthocoridae, especially Oriini, are known to be partly phytophagous.

50. Whereas only the Cimicidae and Polyctenidae are obligatory hematophagous ectoparasites, all Triatominae (Reduviidae) are hematophagous and some *Lyctocoris* species (Lyctocoridae) are at least facultative or possibly obligate blood feeders.